

1 Nutrients on the move: Investigating large scale fatty acid exports
2 from European ponds via emerging insects

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Abstract

105 Permanent ponds represent key landscape components that support biodiversity
106 and supply various ecosystem services. Notably, the export of aquatic subsidies
107 to land via emerging insects, may significantly influence terrestrial food webs.
108 Various factors, including eutrophication, can influence these exports.
109 Polyunsaturated fatty acids (PUFA), which greatly enhance consumer fitness, are
110 among the most important exported components. However, the patterns and
111 drivers of dietary exports from ponds via insects remain poorly known,
112 particularly at continental scales. Here, we analyzed the exports of biomass,
113 lipid, and fatty acid contents from emerging insects, sampled in 36 ponds across
114 11 European countries, over four seasons. We found that both biomass and fatty
115 acid exports decreased with increasing latitude, and were higher in spring and
116 summer. These seasonal effects also increased with higher latitudes.
117 Temperature was the most important predictor of insect biomass, explaining
118 27.6% of the total variation and showing an unimodal response. This suggests
119 increasing temperature may promote exports in colder regions and seasons,
120 whereas it may negatively influence biomass exports in already warm regions.
121 The exports of total lipids, PUFA, and eicosapentaenoic acid were correlated to
122 exported biomass, while those of docosahexaenoic acid were linked to the
123 emergence of Chaoboridae. Moreover, our findings indicated that PUFA contents
124 were affected by taxonomic composition of insect communities and pond trophic
125 state (indicated by *chlorophyll a*). Two of the correlates identified here
126 (temperature and trophic state) are influenced by anthropogenic activity via
127 climate and land use change respectively. Thus, human activity impacts the food
128 webs in and around ponds by influencing the quantity and quality of nutritional
129 exports.

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Keywords

132 freshwater; PUFA; food web; ecology; small water bodies; biomass

134

1. Introduction

135

136 Fluxes of organic matter and nutrients over time and space are important for
137 ecosystem functioning (Barnes et al. 2018), with vectors ranging from desert dust
138 (Prospero et al. 2020) to organisms such as amphibians and insects (Capps et al.
139 2015; Martin-Creuzburg et al. 2017). While the importance of terrestrial subsidies
140 to the aquatic food web has been continuously highlighted (Carpenter et al. 2005),
141 studies of the reverse flow of aquatic subsidies into the adjacent terrestrial
142 environment had been overlooked as inconsequential, however, nowadays plenty
143 of studies show their significance (Nakano and Murakami, 2001; Baxter et al. 2005;
144 Bartels et al. 2012). Research indicates that exported aquatic resources may be
145 critical for terrestrial food webs (Power et al. 2004; Subalusky and Post 2019),
146 however small water bodies, such as ponds, have largely been overlooked (but

147 see Lewis-Phillipps et al. 2020; Fehlinger et al. 2023). This limits our understanding
148 of both the magnitude and nutritious quality of the exports they provide .

149 Ponds are key ecological components of terrestrial environments, providing
150 habitats and valuable ecosystem services (Boix et al. 2012; Hill et al. 2021). Ponds
151 are small water bodies (<5 ha) with shallow water (<5 m) and relatively low cover
152 of emergent vegetation (<30%) (Richardson et al. 2022). Their higher
153 physicochemical heterogeneity compared to larger water bodies, as particularities
154 of their morphology, may promote proportionally higher species richness and
155 provide specific ecological niches, such as clear water habitats or thermal refugia
156 (e.g., Biggs et al. 2017). Further, in addition to being biodiversity hotspots, ponds
157 enable the production of high quantities of insect biomass during the productive
158 season (Dalal and Gupta 2016; Fehlinger et al. 2023).

159 Emerging insects, meaning amphibiotic insects such as Odonata (dragon- and
160 damselflies), which have aquatic larval stages and disperse as flying adults,
161 contribute significantly to the diets of a wide range of terrestrial consumers (e.g.
162 Popova et al. 2017). These subsidies can make up a large portion of the diet of
163 terrestrial consumers, such as resident bird species (25-100%; Baxter et al. 2005;
164 Bartels et al. 2012), bats (Frank et al. 2012), or spiders (Fritz et al. 2017), largely
165 due to a strong preference for aquatic over terrestrial prey (Muehlbauer et al.
166 2014). Overall, the exports vary in quantity, depending on the timing of insect
167 emergence peaks and seasons. This importance and variance of export timing is
168 especially relevant for some consumer species, such as birds, for which aquatic
169 resources play a crucial role during breeding season (Uesugi and Murakami 2007).

170 Aquatic subsidies (i.e., nutrients and/or energy transferred from the aquatic to
171 terrestrial environment), including emerging insects, generally provide a higher
172 nutritional quality, energy density and nutrient concentration than terrestrial
173 subsidies, despite often being lower in quantity (Bartels et al. 2012; Twining et al.
174 2019). This is to a large degree due to the presence of key biomolecules, such as
175 long-chain polyunsaturated fatty acids (LC-PUFA) in aquatic organisms (Napolitano
176 et al 1999; Hixson et al 2015). Among fatty acids (FA), LC-PUFA are essential
177 compounds in food webs, supporting the maintenance, growth, and reproduction
178 of consumers (Brett and Müller-Navarra 1997; Arts and Kohler, 2009). Omega-3
179 (ω 3) LC-PUFAs are of particular note as exported nutrients, including
180 docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), but also
181 arachidonic acid (ARA; an important omega-6 (ω 6) LC-PUFA; Kiene et al., 2023),
182 which are involved in key physiological functions, such as brain function and size
183 (Závorka et al. 2022), inflammatory responses (Tocher 2003) and metabolism
184 (Pilecky et al. 2021). Omega-3 LC-PUFAs are almost exclusively produced by
185 microalgae in aquatic ecosystems (Ahlgren et al. 1990, Napolitano et al. 1999).
186 Emerging insects, like most metazoans, cannot synthesize LC-PUFAs *de-novo*
187 (Kabeya et al. 2018; Malcicka et al. 2018), and must acquire them through diet or
188 from PUFA precursors (Goedkoop et al. 1998; Gladyshev et al. 2013). Evidence
189 indicates that feeding on aquatic prey rich in ω 3 LC-PUFAs (Twining et al. 2021)
190 enhances consumer fitness, growth rate (Marczak and Richardson 2007), immune

191 function (Fritz et al. 2017; Twining et al. 2018), and reproductive success (Twining
192 et al. 2018).

193 While the export quantity of PUFAs from aquatic insects is mainly determined by
194 biomass (Martin-Creuzburg et al. 2017; Scharnweber et al. 2020; Fehlinger et al.
195 2023), PUFA export also depends on specific contributing taxa, among other
196 factors (Parmar et al. 2022). While not the only determinant of FA contents of
197 different species, the feeding strategy has been shown to influence variation in FA
198 profiles (Guo et al. 2018). Thus, community composition strongly determines the
199 quantity and quality supplied to terrestrial consumers (Parmar et al. 2022).
200 Generally, macroinvertebrate community structure is shaped by various
201 parameters, including predator presence, resource availability, water chemistry
202 and waterbody morphology (Biggs et al. 2005; Cereghino et al. 2008; Becerra
203 Jurado et al. 2010). Among aquatic insects, Ephemeroptera (i.e., mayflies) and
204 Chaoboridae (i.e., phantom midges) tend to have the highest levels of EPA and ω 3
205 PUFA (Parmar et al., 2022). For instance, Chaoboridae typically have high levels of
206 DHA, an essential FA for vertebrate physiology that is found in trace amounts in
207 most aquatic insects (Ahlgren et al. 2009; Lau et al. 2012; Martin-Creuzburg et al.
208 2017). In addition to taxa-specific differences, several environmental factors, such
209 as temperature, and anthropogenic pressures, such as land use change, can
210 substantially influence the PUFA content in aquatic insects and transfers to
211 terrestrial ecosystems via direct and indirect pathways (Shiple et al. 2022; Nash
212 et al. 2023; Ohler et al. 2023). As recently highlighted, climate change plays a
213 causal role as a driver of nutritional phenological mismatches between emerging
214 aquatic insects and insectivorous birds (Shiple et al. 2022), with potentially
215 negative consequences for consumer fitness. Indeed, increasing temperatures
216 across seasons and latitudes could alter temperature-controlled emergence
217 patterns of aquatic insects and insect phenologies (Ivković et al. 2013; Forrest
218 2016; Bonacina et al. 2023).

219
220 Additionally, different forms and intensities of land use can strongly affect the
221 export of PUFAs to adjacent terrestrial ecosystems by driving spatiotemporal
222 variation in the composition and phenology of different emerging aquatic insects
223 (Ohler et al. 2023), thus likely influencing food web dynamics in a cross-system
224 context. For example, land use change towards agriculture has previously been
225 linked to increasing trophic state of ponds (Usio et al. 2017), and increased
226 eutrophication and browning can limit the availability of LC-PUFA in aquatic food
227 webs by causing shifts in phytoplankton communities and trophic interactions
228 (Müller-Navarra et al. 2000; Taipale et al. 2016; Senar et al. 2021). Gaining further
229 insights into the amounts and quality of PUFAs exported via emergent insects and
230 how these exports vary along spatial and seasonal gradients is, therefore, crucial
231 to gauge the stability of such a high-quality resource for terrestrial ecosystems.

232
233 Our aim was to advance the current understanding of the spatial and seasonal
234 variation in PUFA export and aquatic insect emergence from ponds. In this study,
235 we focused on the export of insect biomass and dietary energy from permanent
236 ponds covering a broad latitudinal gradient across Europe. We determined this

237 export by quantifying biomass of emerging insects caught with emergence traps,
238 and analyzed their total lipid and specific FA content. Our research investigated
239 the factors influencing these exports, in particular latitude, season, land use, and
240 pond trophic status.

241

242 We hypothesized that temperature, pond trophic state, and surrounding land use
243 significantly influence the biomass and quality of exports by aquatic insects from
244 ponds to adjacent terrestrial environments (Nash et al. 2023; Schell and Kerekes,
245 1989; Greig et al., 2012; Usio et al. 2017; Ohler et al. 2024). More specifically, we
246 expect that:

247 (i) Temperature will drive the biomass of insect exports, with higher exports
248 occurring in warmer seasons (spring and summer) and in regions at lower
249 latitudes;

250 (ii) Pond trophic state will affect both the quantity and quality of exports of fatty
251 acids and biomass, leading to increased biomass and FA exports with higher
252 productivity, but resulting in lower LC-PUFA content per unit of biomass due to
253 reduced algal quality;

254 (iii) Surrounding land use will impact the quantity and quality of FA exports, as
255 ponds in near-natural environments are expected to have different communities
256 compared to those in urbanized environments.

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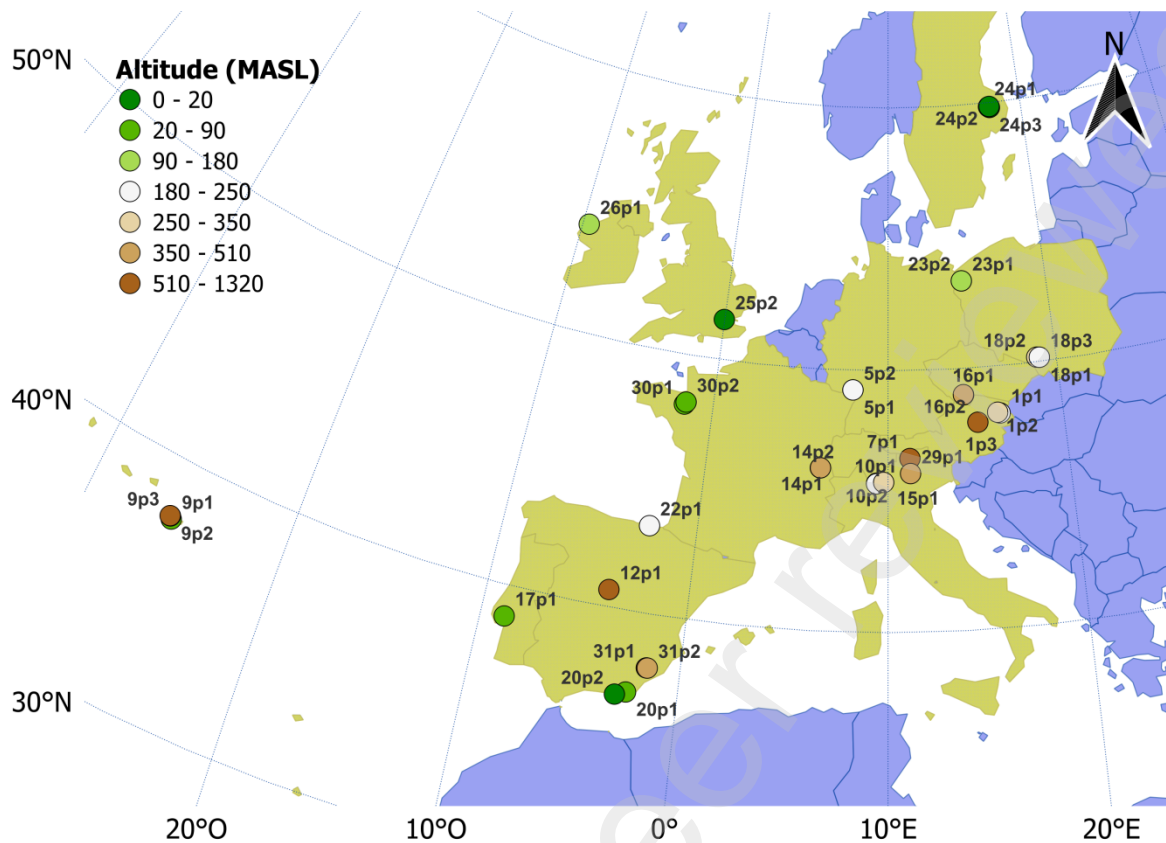
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259 2. Material and Methods

260

261 2.1 Selected study sites and land use categorization

262 Our studied sites included 36 ponds distributed across 11 European countries (Fig.
263 1), covering a wide geographical range, from 36°52'46.64"N in the south (Spain)
264 to 59°51'15.95"N in the north (Sweden) and from -25°46'44.00"W in the west
265 (Portugal) to 19°00'19.4"E in the east (Poland). The climatic conditions show
266 considerable variability between the different regions. In general, the more
267 southern countries have a Mediterranean climate with hot summers and mild, wet
268 winters. Moving north, the climate becomes more temperate with cooler
269 temperatures and more rainfall, influenced by the Atlantic Ocean in the western
270 part. The eastern countries have a more continental climate with cold winters with
271 snow and frost and warm summers.



272
273

274 Figure 1. Distribution of the study ponds (n=36, dot color corresponds to altitude, Pond
275 IDs consist of team number, p for pond, number of sampled ponds per team selected for
276 field work across 11 different European countries (studied countries are green).
277

278

279 In each country, one to seven ponds were chosen for sampling on the basis of
280 water permanence, depth and accessibility, with all ponds maintaining water
281 throughout the year and having a maximum depth of 3 m (0.5 - 3.0 m) (Table S1).
282 The ponds were mostly of artificial origin, different ages, and at different altitudes
283 (1 - 1322 MASL; Table S1; Fig. 1). Based on in situ observations, 67% of the ponds
284 contained fish while the rest were fish-free (Table S1). Land use in the adjacent
285 terrestrial ecosystem surrounding the study ponds was calculated with a 100m
286 and 1000m buffer (radius) from the pond centroid (Thornhill et al. 2017), using the
287 Corine Land Cover (CLC) 2018 database (scale 1:100.000; EEA 2018). We
288 reclassified all CLC land use categories into 5 terrestrial groups to facilitate the
289 interpretation: urban, agricultural, forest, open habitats and water (Table S1).

289

290 2.2 Emerging insects sampling

291 Aquatic emerging insects were sampled two times within the same week in each
292 pond in three day intervals. This was repeated in each season from autumn 2020
293 to summer 2021 (4 sampling periods scattered over a full annual cycle). Data on
294 insect emergence at the study ponds were collected using pyramid-shaped
295 floating emergence traps. These traps consist of a net (~500 µm) fixed to a PVC-
296 pipe structure and crowned by an external collection bottle (Fig. S1), as described

297 by Cadmus et al. (2016). To maximize representativeness of insect samples,
298 emergence traps were intentionally deployed to cover all representative habitats
299 within each pond, with one to three traps covering a total surface area of 0.54 to
300 3 m². The traps were checked and manually emptied twice per week (on days 3
301 and 7 after deployment) to ensure that samples were not too degraded for
302 biochemical analysis. The samples were transported to the laboratory and frozen
303 (at or below -20°C), and freeze-dried for analysis. The emerging insects were
304 identified under stereo-microscopes using national- or regional-level identification
305 keys (Selection of used literature in the Supplementary Material) to the lowest
306 possible taxonomic level, usually family or order level.

307

308 2.3 Observational and physicochemical data collection

309 During each sampling event, the teams measured electric conductivity, dissolved
310 oxygen, oxygen saturation, water temperature, pH, and water transparency
311 (measured by Secchi depth). Additionally, the teams visually assessed the
312 heterogeneity of the pond bed by estimating the relative abundance of six
313 substrate categories, and percentage of surface covered by submerged and
314 emergent macrophytes (Table S1). Further, weather data (sunhours, precipitation,
315 maximum and minimum air temperatures) were recorded for the sampling day
316 and three preceding days (Table S1). Fish presence was noted at each site (Table
317 S1). *Chlorophyll a* concentration was measured either *in situ*, alongside other
318 physical and chemical parameters) or in the lab.

319

320 2.4 Fatty acids analysis and sample selection

321 Lipids were extracted following Heissenberger et al. (2010). Total lipid (TL)
322 contents expressed as mass fractions (mg TL g DW⁻¹, where DW is dry weight),
323 were obtained by gravimetry: dropping 100 µL of the extract into pre-weighed tin
324 capsules, and re-weighing them after the liquid extract had evaporated. Following
325 extraction, a portion of the total lipids was transmethylated to produce FA methyl
326 esters (FAME), which were subsequently analysed using a gas chromatograph
327 (Trace GC; Thermo Scientific; FID 250°C, carrier gas: He: 1 ml min⁻¹, detector
328 gases: H₂: 35 ml min⁻¹, make-up gas flow 30 ml min⁻¹, air: 350 ml min⁻¹,
329 temperature ramp of the oven: 140°C at 20°C min⁻¹ for 5 min, to 170°C at 4°C
330 min⁻¹ and to 240°C at 2°C min⁻¹ for 8 min), equipped with a flame-ionization
331 detector (FID, set at 250°C). The FAME were separated using a Supelco SP-2560
332 column (100 m, 0.25 mm i.d., 0.2 mm film thickness). Their retention times were
333 compared with standards (37-component FAME Mix, Supelco 47885-U; Bacterial
334 Acid Methyl Ester Mix, Supelco 47080-U) and quantified by reference to seven-
335 point calibration curves based on known standard dilution raw concentrations. All
336 fatty acids were measured and reported as FAME. Their contents were expressed
337 as mass fractions (mg FAME g DW⁻¹) and mass percentages (%) of total reported
338 fatty acids. Some samples could not be analyzed due to low sample quantity (< 2
339 mg DW). To prevent the removal of entire ponds due to missing values in a small
340 portion of their biomass export, we extrapolated the TL and fatty acid content of
341 those samples from the TL and FA means in the entire dataset.

342 This is based on the assumption that the majority of the variation of fatty acid
343 exports is driven by differences in quantities of biomass exported (Martin-
344 Creuzburg et al. 2017; Scharnweber et al. 2020).

345 2.5 Data processing

346 We unified differences in taxonomic levels before conducting statistical analysis,
347 leading to the following categories: Chaoboridae, Chironomidae (i.e., non-biting
348 midges), Ephemeroptera (i.e., mayflies), and Odonata (i.e., damselflies and
349 dragonflies). Taxa that contributed less than 5% in biomass and lipid exports were
350 classified as “Others” (including Trichoptera, Coleoptera, Culicidae, other
351 unspecified Diptera, Hemiptera, Lepidoptera, Neuroptera, Plecoptera and 3
352 unidentified taxa; Table S2). The data was processed, analyzed, and visualized
353 using R (v4.3.1, R Core Team 2022). Response variables included biomass (mg per
354 $\text{m}^2 \text{ day}^{-1}$), total fatty acids (TFA) and total lipids (TL) per pond and sampling season.
355 In addition, we investigated the drivers for specific fatty acids (ARA, EPA) and total
356 PUFA in mg g^{-1} . The omega-3/omega-6 PUFA ratio (ω_3/ω_6) was used as a proxy for
357 the quality of fatty acid composition. The biomass exported from each pond during
358 a specific season was calculated by dividing the DW of the collected sample (in
359 mg) by the product of the area sampled by the emergence traps (in m^2) and the
360 number of days the traps were active.

361 $\text{biomass} = \text{DW in mg} / (\text{area sampled in m}^2 * \text{number of days})$

362 To calculate total lipid and FA exports, the contents (in mg g^{-1} biomass) were
363 multiplied by the sample biomass (in g) and standardized by pond surface area
364 and number of days of trap deployment. Then, to calculate the contribution of TL
365 and the different FA and FA groups to the exports, we divided the different FA and
366 TL exports by the biomass export for each sampling and we multiplied the result
367 by 100 to express them as percentage. Exports ($\text{mg day}^{-1} \text{ m}^{-2}$) and contents (mg
368 g^{-1} DW) were $\log_{10}(x)$ transformed; for export variables including zeroes, we used
369 a $\log_{10}(x+0.1^i)$ -transformation i , where i was chosen based on the order of
370 magnitude of each variable: biomass export ($i=1$), TL export ($i=2$), PUFA export
371 ($i=4$), EPA export ($i=4$), DHA export ($i=5$), DHA content ($i=2$). All numerical
372 explanatory variables were standardized by centering them around the mean and
373 dividing them by their standard deviation.

374 We summarized the main land-use gradients in our dataset by performing a
375 principal component analysis of land-use classes at 100m and 1000m radius using
376 the *vegan* package in R (Oksanen et al. 2022). We extracted the site scores of the
377 two first principal components, which explained 62.0% of the variation in land use
378 (Fig. S2). The first principal component (PC1_urban; 35.3% of the variation) is a
379 proxy for urbanization and low forest cover, while the second principal component
380 (PC2_agriculture; 27.7% of the variation) is a proxy for agriculture (Fig. S2).

381

382 2.6 Statistical analysis

383 To test the effects of different drivers on quantities and FA composition of exports,
384 linear mixed effect models were fitted using the *lmer* function in the *lme4* package
385 (Bates et al. 2015). For statistical testing, we used the *lmerTest* function (*lmerTest*
386 package; Kuznetsova et al. 2017) with Kernward-Rogers estimate of degrees of
387 freedom. To test pairwise differences among factor levels and among interaction
388 slopes, we used the *emmeans* and *emtrends* function, respectively, from the
389 *emmeans* package (Lenth et al. 2024), which estimates marginal means (EMMs)
390 using TukeyHSD correction. We calculated the marginal (R^2_m) and the conditional
391 (R^2_c) coefficient of determination, which represents the proportion of the variation
392 explained by the fixed effects and the whole model respectively (Nakagawa et al.
393 2017), using the *r.squaredGLMM* function in *MuMIn* package (Barton and Barton
394 2015). We also calculated the semi-partial R^2 , as an estimate of the variation
395 explained by each of the model predictors, using *partR2* function from the *partR2*
396 package (Stoffel et al. 2021) with 10 parametric bootstrap iterations. Finally, we
397 visually inspected diagnostic plots for residuals of the final models for verifying
398 model assumptions, and we checked for multicollinearity based on variance
399 inflation factors using the *car* package ($VIF < 3$) (Zuur et al. 2009; Fox and
400 Weisberg 2019).

401 2.6.1 Biomass, lipid and fatty acid export analysis

402 To study the drivers of biomass exports, we took two different approaches. First,
403 we used a linear mixed effects model with Pond ID as a random intercept fitted by
404 REML (restricted maximum likelihood) with (see 2.5.1. Data processing) to assess
405 the contribution of spatial (latitude and elevation) and temporal (season) variation
406 to the biomass exports ($n_{\text{datapoints}}=118$, $n_{\text{ponds}}=36$). As latitude was highly correlated
407 with longitude (Fig. S3, $r_s=0.77$, $p<0.001$), only latitude was included in the model
408 as proxy for both latitudinal and longitudinal changes. Additionally, we ran a model
409 including latitude*season and altitude*season interactions to test for differences
410 in seasonality patterns in emergence across spatial gradients. To estimate
411 latitudinal trends of exports for each season, we performed linear regressions with
412 latitude as predictor on datasets subsetted by season.

413 Then, we investigated which environmental drivers explained spatial and seasonal
414 variation in biomass exports. To do that, we fitted linear mixed models with
415 quadratic terms to inspect non-linear responses (see 2.5.1. Data processing; see
416 Table S3 for model equations and results) in growing complexity: our simplest
417 model included general bottom-up drivers (i.e., temperature and chlorophyll *a* (mg
418 L^{-1}), as a measure of the pond's trophic status) and top-down (fish presence)
419 drivers of overall secondary production of aquatic insects. To that model, we added
420 other sets of variables that may regulate emergence, e.g. water chemistry
421 (conductivity ($\mu\text{S cm}^{-1}$)), habitat size and land use (pond size (m^2), PC1_urban,
422 PC2_agriculture), and the combination of both, resulting in four different models
423 in total (for this analysis $n_{\text{datapoints}}=90$). Then we selected the best model based on
424 the lowest Akaike Information Criterion (AIC) using the *anova* function, and we
425 determined the suitability of other models to be valid alternatives based on AIC
426 differences (ΔAIC), whereby $\Delta\text{AIC} < 2$ indicates 'substantial' support (Burnham &

427 Anderson, 2002). In this analysis and henceforth, we excluded other variables (e.g.
428 macrophyte cover, oxygen concentration, pH) due to a high degree of missing
429 values that would result in high reductions of degrees of freedom below 75% of
430 the original number of data points ($n=118$). Potential contributions of the
431 eliminated variables to the biomass export were assessed post-hoc, via their
432 correlations with the exports and/or the significant environmental predictors (Fig.
433 S3).

434 To further assess the general predictive power of biomass on lipid and FA exports,
435 we performed linear models, with biomass export as predictor of TL, PUFA, EPA
436 and DHA ($n=89$) and inspected the coefficient of determination (R^2). Chaoboridae
437 biomass has been previously identified as an important predictor for DHA exports
438 (Martin-Creuzburg et al. 2017). Accordingly, we fitted two additional linear models
439 to assess the effect of Chaoboridae biomass on DHA export: (1) a model with both
440 whole community biomass and Chaoboridae biomass as linear predictors of DHA
441 exports ($n=89$), and (2) a model of Chaoboridae biomass as a linear predictor of
442 DHA exports, in samplings where Chaoboridae were present ($n=13$).

443 2.6.2 Taxonomic and environmental drivers of quality of export

444 We defined the nutritional quality of export as the contents of lipids, PUFA, EPA
445 and DHA per unit of exported biomass (mg/g DW) and as the $\omega 3/\omega 6$ PUFA ratios.
446 First, we tested for taxonomic differences in lipid and fatty acid contents (i.e., TL,
447 PUFA, DHA, EPA) and $\omega 3/\omega 6$ PUFA ratios using a linear mixed effects model with
448 taxon group as a fixed effect, followed by post-hoc tests for pairwise comparisons
449 (See 2.5.1. Data processing). In order to assess the relative importance of each
450 insect group to the different types of exports, we also summed the total exports
451 in biomass, DHA, EPA, $\omega 3$, $\omega 6$, PUFA, TL for each taxon, and calculated their
452 percentage contribution to the total biomass, DHA, EPA, $\omega 3$, $\omega 6$, PUFA, and TL
453 exports, respectively. To further understand how taxonomic differences in fatty
454 acid composition affect the quality of exports, we first performed constrained
455 multivariate analysis (MVA) in the *vegan* package in R (Oksanen et al. 2022),
456 aiming to assess broad changes in the community biomass composition in our
457 dataset. Preliminary detrended correspondence analysis (DCA) showed gradient
458 lengths of 2.32 and 2.52 for the two first axes, respectively, supporting the choice
459 of RDA over unimodal ordination methods (Ter Braak and Prentice 1988; Lepš and
460 Šmilauer 2003). Environmental predictors in the RDA were water temperature, fish
461 presence, pond size, conductivity, chlorophyll *a*, and the first two principal
462 components of land use ($n=74$). We tested the marginal effects of environmental
463 predictors using an ANOVA test with 999 permutations, and variation explained by
464 the environmental predictors was calculated by multiplying the variance term from
465 the ANOVA table times the inertia of the RDA model (e.g. Lau et al. 2012).

466 Finally, we assessed the effects of taxonomic and environmental drivers on the
467 quality of exports, as the contents (mg g⁻¹ DW) of total lipids and important fatty
468 acids (i.e., PUFA, EPA, DHA), and as $\omega 3/\omega 6$ ratios. To do that, we used linear mixed-
469 effect models including the relative biomasses of the major represented insect
470 taxa (i.e., Chaoboridae, Chironomidae, Ephemeroptera and Odonata) as fixed

471 effects and environmental drivers (i.e., chlorophyll *a*, conductivity, water
472 temperature, pond size, fish presence and the first two principal components of
473 land use) as predictors.

474 3. Results

475 3.1. Ranges of biomass, total lipid and fatty acid exports

476 Biomass exports via emerging insects were variable among ponds across Europe
477 (Table S4) and within ponds across seasons (Table S5), and ranged from 0 mg DW
478 m⁻² d⁻¹ in autumn and winter at high latitudes, where many ponds were frozen
479 (Table S4, Table S5), to 208.2 mg DW m⁻² d⁻¹ in a productive pond during the
480 summer (pond 10p2, Italy; Fig. 1, Table S4). Lipid exports were on average 14.9%
481 (± 6.2 SD) of the biomass exports, whereas PUFAs represented 2.63 % (± 1.3 SD)
482 (Table S6). Exports of EPA ranged between 0 and 2.95 mg DW m⁻² d⁻¹, while DHA
483 exports were more than one magnitude lower (Table S5) and below detection
484 limits in 15 of the 89 pond-per-season samples used for FA analysis. On average,
485 $\omega 3$ exports from our ponds were higher than $\omega 6$ exports ($\omega 3/\omega 6 > 1$, Table S5), and
486 the $\omega 3/\omega 6$ ratio varied greatly among ponds (range 0.3–4.8), but not among
487 seasons (Table S5).

488

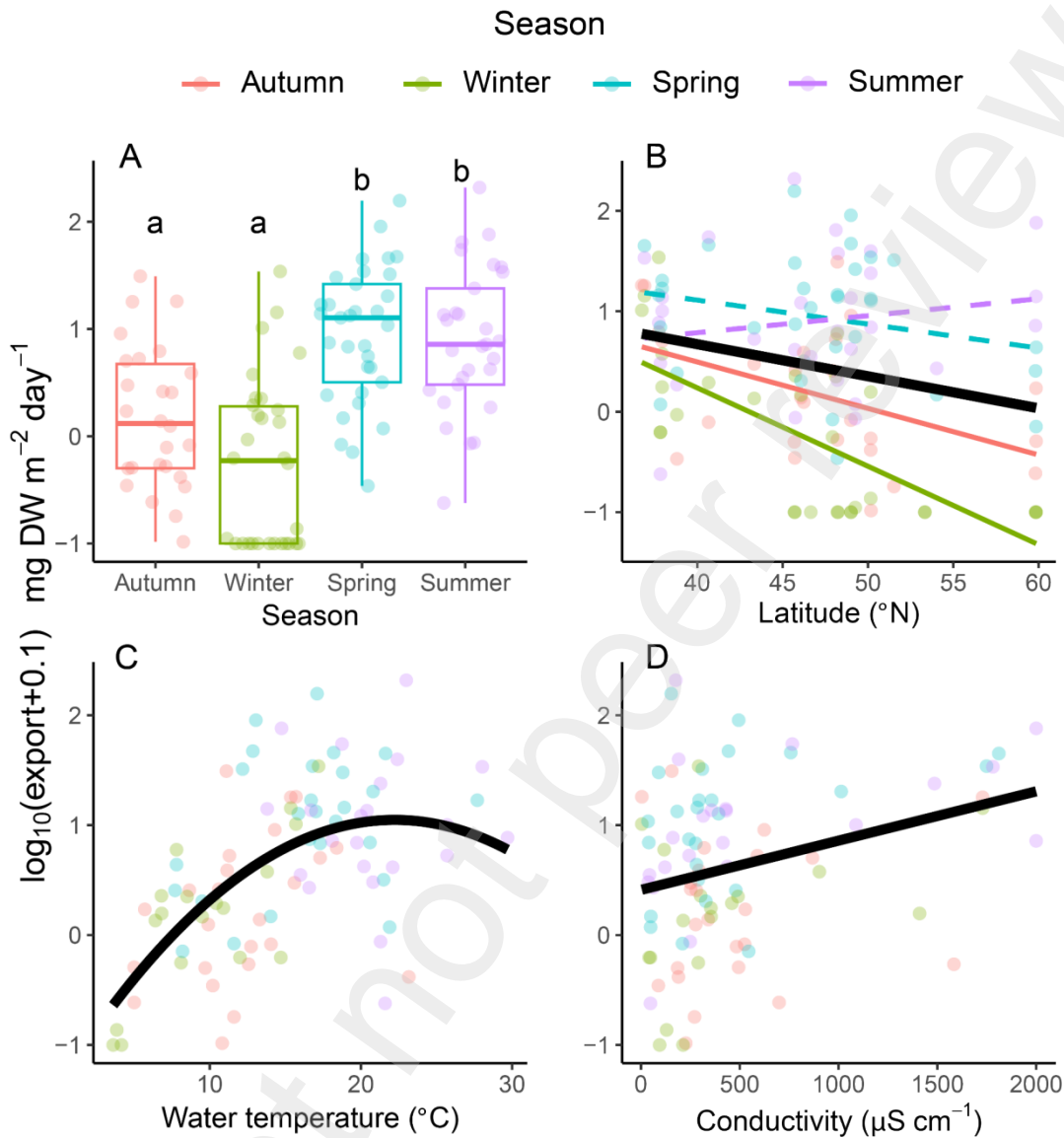
489 3.2. Drivers of biomass, total lipid and fatty acid exports

490 Spatial and seasonal predictors (i.e., latitude, altitude and season) explained
491 50.2% of biomass export variation (R^2_{mi} ; Table 1A), with significant effects of
492 season and latitude, but not of altitude (Table 1A). Season explained the vast
493 majority of the biomass exports (36.0%, semi-partial R^2 ; Table 1A), showing higher
494 exports in spring and summer than in the other seasons (Tukey HSD in model
495 without interactions, $p < 0.001$, Fig. 2A), and marginally higher exports in autumn
496 than in winter (Tukey HSD in model without interactions, $p = 0.07$, Fig. 2A). Latitude
497 had an overall negative effect on biomass exports (Table 1A, Fig. 2B). However,
498 the effect of latitude was dependent on season (significant season:latitude
499 interaction; Table 1A) with steeper slopes in winter than in spring ($\Delta_{\text{Winter-Spring}} =$
500 -0.15 ± 0.06 , $p = 0.046$) and summer ($\Delta_{\text{Winter-Summer}} = -0.24 \pm 0.06$, $p < 0.001$). This
501 season interaction term explained 7.7% of the variation in biomass exports (semi-
502 partial R^2 ; Table 1A). Single linear models per season showed decreases in biomass
503 exports with latitude in winter (slope = -0.18 ± 0.04 , $F_{1,28} = 23.8$, $p < 0.001$, $R^2 = 0.46$)
504 and autumn (slope = -0.11 ± 0.04 , $F_{1,24} = 6.3$, $p = 0.016$, $R^2 = 0.21$), while no
505 significant trends were found in spring (slope = -0.05 ± 0.04 , $F_{1,31} = 1.8$, $p = 0.18$,
506 $R^2 = 0.06$) or summer ($F_{1,27} = 0.8$, $p = 0.38$, $R^2 = 0.03$).

507 In the study of the environmental drivers of the biomass exports, the model
508 including bottom-up drivers (water temperature, chlorophyll *a*), top-down drivers
509 (fish presence), and water chemistry (i.e., conductivity) was the best fit model
510 (Table S3). Water temperature explained most of the variation (27.6%; semi-
511 partial R^2 ; Table 1B) and had a significant quadratic relationship ($R^2_m = 0.385$,
512 $p < 0.001$ Fig. 2C; Table 1B). Neither chlorophyll *a*, as a proxy for trophic status, nor
513 fish presence significantly affected the biomass exports (Table 1B). Conductivity,

514 on the other hand, had a significant positive effect on biomass exports (Fig. 2D),
515 explaining 3.7 % of the variability (semi-partial R^2 $p < 0.05$; Table 1B).

516



517

518 Figure 2. Effect of A) season, B) latitude, C) water temperature and D) conductivity on
519 biomass export. In A), different letters indicate significant differences ($p < 0.05$) among
520 seasons, on the basis of linear models followed by pairwise multiple comparisons. In B),
521 the thick, black line represents the overall effect of latitude and dashed lines represent
522 non-significant trends. For A) and B), $n = 118$; for C) and D), $n = 90$. Boxplots depict median,
523 25th and 75th percentile, and whiskers extend to maximum and minimum values.

524

525 While biomass significantly explained the majority of variation in exports of TL,
526 PUFA, EPA, and was also a highly significant predictor for DHA exports ($p < 0.001$,
527 Table S7), the predictive power of biomass to DHA export was lower than other
528 lipid exports investigated ($R^2 = 0.66$, Table S7). Including Chaoboridae biomass in
529 the regression model increased the goodness of fit of the model by 10% ($R^2 = 0.76$,

530 intercept= -7.87 ± 0.30 , $\text{slope}_{\text{biomass}} = 0.84 \pm 0.06$, $\text{slope}_{\text{Chaoboridae}} = 0.83 \pm 0.12$,
531 $p < 0.001$). When Chaoboridae were present, Chaoboridae biomass export
532 predicted 82% of the variation in pond DHA exports ($R^2 = 0.82$, intercept=
533 5.62 ± 0.26 , slope= 1.15 ± 0.16).

534
535

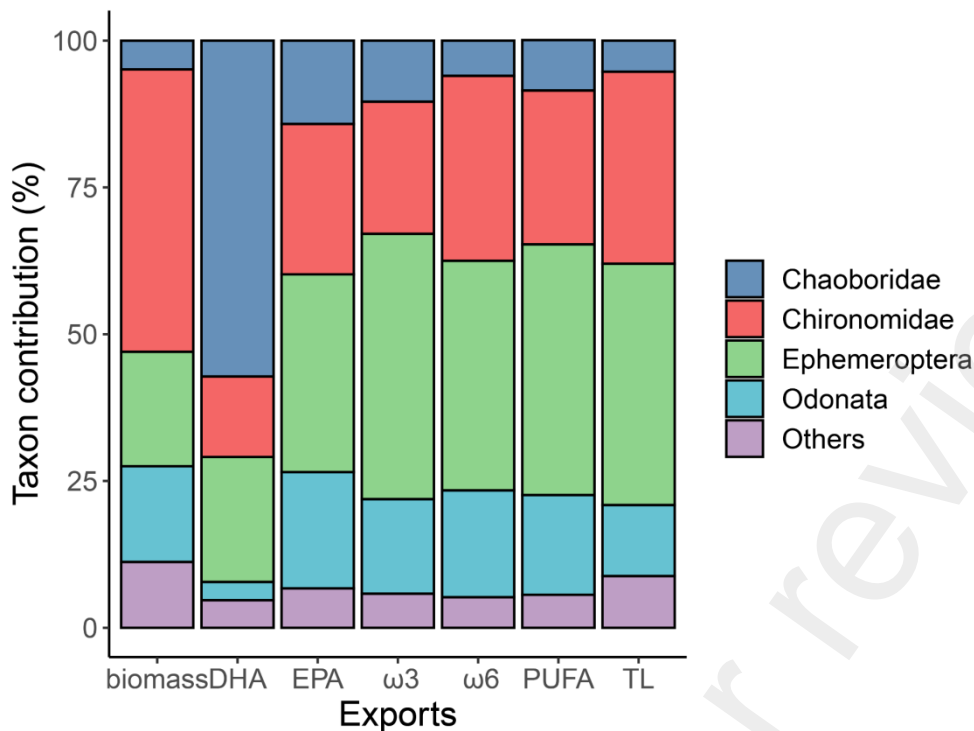
536 3.3. Taxonomic differences

537 Contents of the different lipids and fatty acids differed among taxa (Mixed ANOVA:
538 $F = 19.1$ to 29.9 , $p < 0.01$; Fig. S4; Table S8). Chaoboridae were characterized by
539 high DHA contents $2.6 \pm 2.5 \text{ mg g}^{-1} \text{ DW}$ (mean \pm SD), while the other taxa had values
540 $< 0.3 \text{ mg g}^{-1} \text{ DW}$ (Fig. S4, Table S2). Ephemeroptera had the highest PUFA
541 ($61.1 \pm 32.1 \text{ mg g}^{-1} \text{ DW}$) and total lipid contents ($270.4 \pm 115.7 \text{ mg g}^{-1} \text{ DW}$), and also
542 the highest EPA contents ($14.3 \pm 5.5 \text{ mg g}^{-1} \text{ DW}$) along with Chaoboridae (14.9 ± 7.5
543 $\text{mg g}^{-1} \text{ DW}$) (Fig. S4, Table S2). Chironomidae, Trichoptera, Odonata and other taxa
544 presented generally lower contents of the different lipids, and lower $\omega 3/\omega 6$ ratios
545 than Chaoboridae and Ephemeroptera (Fig. S4; Table S2).

546

547 Ephemeroptera was the taxon that contributed the most to TL (41.1%), PUFA
548 (42.7%), omega-3 (45.2%), omega-6 (39.1%) and EPA (33.7%) exports despite
549 having a lower share of the biomass (19.5%, Fig. 3, Table S2). This is corroborated
550 by the very high TL, PUFA, and EPA contents in Ephemeroptera (Fig. S4). On the
551 other hand, Chironomidae had a high contribution to biomass exports (48.1%), but
552 lower contributions to TL exports (13-32%, Fig. 3), which aligns with their overall
553 low TL contents (Fig. S4). DHA exports were highly dependent on Chaoboridae
554 midges, which represented 57.2% of the total DHA exports while only contributing
555 to 4.9% of the biomass export (Fig. 3). Chaoboridae emergence was only detected
556 in 13 of the 101 samples (12.8%) and in 11 of the 36 ponds (30.5%) with FA exports
557 analysed. Other taxa contributing to $>10\%$ of the DHA exports were
558 Ephemeroptera (21.3%) and Chironomidae (13.7%) (Fig. 3), but samples of both
559 taxa generally had lower DHA contents than sampled Chaoboridae (Fig. S4). Note
560 that the high contribution of Ephemeroptera to DHA export is only based on one
561 sample (Fig. S4).

562



563

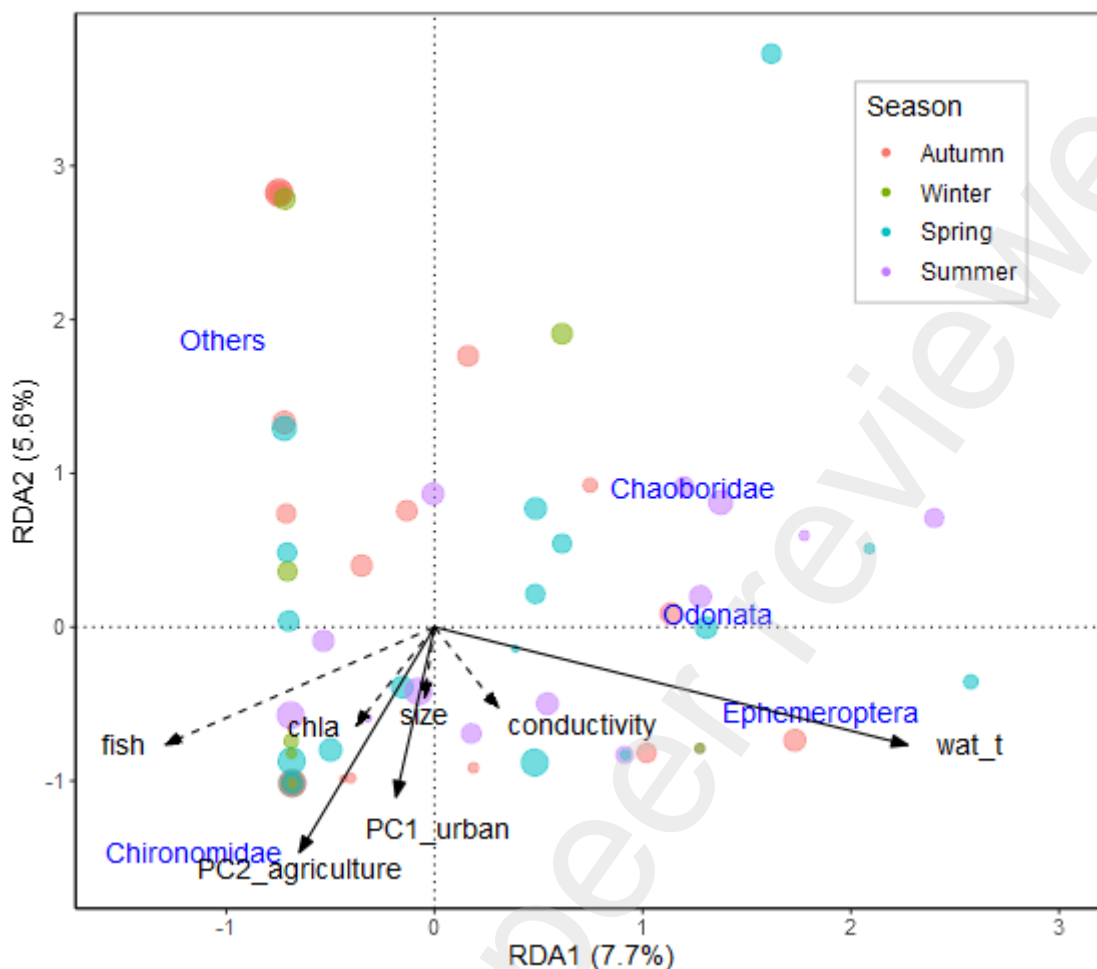
564 Figure 3. Contribution of different taxa to the different types of exports as by percent of
 565 the total exports, where "Others" are the pooled taxa that individually contributed to less
 566 than 5% in any of the exports. ω3 = omega-3, ω6 = omega-6.

567

568 3.4. Drivers of export quality

569 According to redundancy analysis (RDA), environmental variables (water
 570 temperature, fish presence, pond size, chlorophyll *a*, conductivity and land use)
 571 explained 14.7% of all the variation in the community composition of insect
 572 emergence (Table S9). Of all the variables, only water temperature (Fig. 4)
 573 significantly contributed to the RDA model (ANOVA, $F=(1.66, 4.28)$, $p=0.003$,
 574 Table S9) and explained 4.58% of the variation, while the proxies for urbanization
 575 and agricultural land use were marginally significant (PC1_urban, $F=(1.66, 2.10)$
 576 $p=0.072$; PC2_agriculture; $F=(1.66, 2.27)$ $p=0.054$; Table S9). Agricultural and
 577 urban land use proxies were positively correlated with relative biomass of
 578 Chironomidae. Likewise, forest land use, denoted by a negative PC1_urban, was
 579 correlated to occurrence of Chaoboridae and "Others" (Fig. 4; Table S9).

580



581
 582 Figure 4. Redundancy analysis of the community composition of emerging insects in
 583 response to environmental drivers (n=74). Blue names represent eigenvectors of insect
 584 taxa. Symbol size is directly proportional to latitude. Black arrows and names represent
 585 the eigenvectors of environmental variables included in the model, where solid arrows
 586 represent significant predictors $p < 0.05$. wat_t = water temperature, chla = chlorophyll a,
 587 conductivity = conductivity, fish = fish presence, PC1_urban = proxy for urbanization,
 588 PC2_agriculture = proxy for agricultural land use, size = pond size
 589

590 Taxa displayed different FA compositions, which further predicted varying lipid
 591 contents, which in turn affected lipid contents per unit of biomass. TL contents and
 592 total PUFAs were positively associated with the contribution of Ephemeroptera in
 593 the emergence community. For EPA, we found positive effects of the contribution
 594 of Ephemeroptera, Chaoboridae and Odonata, which were high in EPA contents
 595 (Table 2, Fig. 4). However, the models also suggested a significant positive effect
 596 of Chironomidae contribution, even though this taxon generally did not have high
 597 EPA contents (Table 2, Fig. 4). Further, $\omega 3/\omega 6$ ratios of the exports were positively
 598 affected by the dominance of Ephemeroptera and Odonata (Table 2). As pointed
 599 out in previous sections, most of the DHA contents were positively related with the
 600 relative biomass of Chaoboridae in the emerging community (Fig. 4). Once
 601 accounting for the effects of taxonomic composition, we also found significant
 602 effects of environmental drivers on lipid contents of the exported biomass. Those
 603 consisted most notably in a positive effect of chlorophyll a on PUFA and EPA
 604 contents (Table 2).

605

607 4. Discussion

608

609 We found that the effects of season, latitude and longitude explained 50.2% of
610 biomass exports across Europe, with high variability, influenced by water
611 temperature and conductivity. TL, PUFA and EPA exports correlated with biomass
612 and were thus heavily driven by the occurrence of larger (or maybe heavier) taxa,
613 such as Ephemeroptera, while the export of the essential DHA was mainly driven
614 by the presence of Chaoboridae. This taxonomic discrepancy held true across the
615 spatial scale studied, highlighting the importance of insect community
616 composition in delivering different FA profiles from permanent ponds to the
617 terrestrial environment, across the entire continent. Overall, this study highlights
618 the pivotal role of ponds in distributing essential resources across a broad
619 geographical scale, thereby emphasizing their significance as fundamental
620 ecosystems within the landscape (Biggs et al. 2017). The strong influence of
621 temperature suggests that this resource provisioning is highly susceptible to rises
622 of temperature and increases of temperature fluctuations (i.e. heat waves, cold
623 waves) in response to climate change. Our study represents the first
624 comprehensive investigation at continental scale of both the quantity and quality
625 of emerging insect exports, considering both spatial and seasonal dynamics.

626

627 **Effect of season and temperature on biomass and FA exports**

628

629 We observed higher exports of insect biomass in spring and summer across all
630 countries. Interestingly, the effect of season depended on latitude, with exports at
631 higher latitudes being most affected by seasonality. Consequently, biomass
632 exports in colder months and at higher latitudes were the most affected. This can
633 be due to temperature, which limits most biological rates including biomass
634 production (Brown et al 2004). Temperature has stronger fluctuations at higher
635 latitudes, and thus influences seasonal fluctuations in emergence (e.g. Nash et al.
636 2023). We recorded an export of biomass equal to an average around 13 mg DW
637 $\text{m}^{-2} \text{d}^{-1}$, however, the range of values recorded was rather large. Comparing our
638 data with existing literature is challenging due to the limited number of
639 publications focusing on insect emergence from ponds. Still, our biomass exports
640 in summer ($21.6 \pm 45.7 \text{ mg DW m}^{-2} \text{d}^{-1}$) are comparable to those reported in two
641 recent studies conducted in eutrophic fish ponds in Austria ($\sim 13.6 \text{ mg DW m}^{-2} \text{d}^{-1}$,
642 June - September, Fehlinger et al. 2023) and in managed farm ponds in the UK (52
643 $\text{mg DW m}^{-2} \text{d}^{-1}$, May, Lewis-Phillips et al. 2020). However, our sampling campaigns
644 were not timed explicitly to capture emergence peaks, so we may have
645 underestimated the exported biomass and amount of exported fatty acids in our
646 dataset, especially in the more productive seasons.

647

648 Our findings that biomass and, therefore, nutrient transfers are the highest during
649 spring and summer, are in line with previous studies (Nakano and Murakami 2001;
650 Uesugi and Murakami 2007). Especially in ponds that were frozen in winter, such
651 as in Sweden, Austria, Germany, or Czech Republic, the only relevant amounts of

652 exported essential nutrients were recorded in the spring and summer months.
653 Particularly in harsh and cold environments with short growing seasons, emerging
654 aquatic insects can adapt to have synchronised diapauses during the ice-cover
655 time of the ponds, to optimise the timing of emergence for an ideal reproductive
656 phase (Lencioni 2004). These patterns observed on a continental scale highlight
657 the importance of understanding existing patterns of emergence, especially under
658 the circumstances of ongoing climate change impacting those processes. For
659 example, multiple studies have associated the insect emergence timing and
660 vulnerable times in consumer life cycles, such as during the breeding season of
661 tree swallows (*Tachycineta bicolor* Vieillot, 1807; Twining et al. 2018). These
662 findings reiterate the importance of aquatic-derived biomass and nutrients for
663 terrestrial consumers considering that terrestrial prey are scarce during certain
664 important phases (Nakano and Murakami 2001) and that both terrestrial and
665 aquatic insects are not nutritionally equal (Twining et al. 2019). Aquatic insects
666 contain significantly higher levels of LC ω 3-PUFA (Schindler and Smits 2017; Lewis-
667 Phillips et al. 2020). Climate change-induced decoupling between the timing of
668 insect emergence and the demand of terrestrial consumers, who rely on these
669 essential aquatic resources, could lead to negative consequences along the entire
670 trophic chain (Shiple et al. 2022).

671 The unimodal response of emergence to increasing water temperature hints at the
672 temperature sensitivity of insect emergence and suggests potential alterations
673 under climate change conditions. In general, insect emergence was higher in
674 warmer regions and seasons at lower latitudes compared to colder regions and
675 seasons. However, the unimodal relationship indicates that colder regions and
676 seasons could benefit from warming conditions, while warmer regions and seasons
677 are likely to remain either constant or be negatively affected by increasing
678 temperatures. The patterns of this latitudinal and climatic dependence have been
679 observed globally (Nash et al. 2023), resulting in strong seasonal effects,
680 particularly in ponds located at higher latitudes. In previous studies, water
681 temperature also had a highly significant positive relationship with emerging
682 insect abundance (Salvarina et al. 2017; Lewis-Phillips et al. 2020). Our data
683 suggests that the positive effects of temperature on emergence induction might
684 dampen above 20°C of water temperature. This might adversely impact exports
685 from more southern countries in the warmer months, where temperatures
686 frequently surpass those temperature optima.

687 **Effect of land use and community composition on biomass and FA exports**

688
689 Regarding the impacts of water chemistry, conductivity was found to positively
690 influence biomass exports. Previously, higher conductivity, which sometimes was
691 used also as a proxy for salinity, has been linked to increased species richness and
692 abundance of certain taxa, including many generalist taxa such as the dragonfly
693 genus *Ischnura* (Jooste et al. 2020), thus directly influencing community
694 composition. Indeed, increased conductivity has also been linked to increased
695 shares of arable land, directly connecting land use and water conductivity levels
696 (Kupiec et al. 2021). Additionally, higher conductivity has previously been listed
697 as a land-use related driver of aquatic insect emergence. Our study recorded a

698 positive correlation between increasing agriculture, urbanization and
699 Chironomidae biomass, and between increased forest, Chaoboridae biomass and
700 the taxa grouped as "Others". Findings by Ohler et al. (2023) are similar to ours,
701 having found more Chironomidae biomass exported at agricultural than forested
702 sites. While many factors influence the community composition of aquatic insects,
703 considering the proposed links between land-use change and insect community
704 assemblages warrants future deep investigations of environmental drivers
705 influencing shaping communities and therefore the nutrients exported.

706 The amounts of nutrients transferred were largely correlated with biomass
707 transfer; however, DHA exports were mainly explained by Chaoboridae presence
708 (82% of variation explained). This is very much in line with findings from Martin-
709 Creuzburg et al. (2017), which reported the same relationship from a German lake.
710 However, our results confirm the correlation between DHA exports and
711 Chaoboridae occurrence in ponds at a continental scale. According to our findings,
712 almost 50% of exports were made up of Chironomidae, which have previously
713 been found to make up the majority of exported biomass from ponds (Fehlinger et
714 al. 2023), lakes (Martin-Creuzburg et al. 2017) and streams (Baxter et al. 2005).
715 While Ephemeroptera (~20%), Odonata (~16%) and Chaoboridae (~5%) made up
716 smaller portions of the total biomass exported, their contributions to the overall
717 FA exported were considerable. In general, the mayflies (Ephemeroptera) and
718 midges (Chaoboridae) tend to have the highest amounts of EPA and omega-3
719 PUFA, highlighting the importance of diverse communities for the export of dietary
720 energy, emphasizing the ecological role of different taxa in terms of their FA
721 profiles (Parmar et al. 2022).

722

723 **Pond trophic state and the quantity and quality of biomass and FA** 724 **exports**

725

726 Among the factors that could be assumed to influence aquatic insect emergence,
727 neither *chlorophyll a* nor fish presence seemed to impact biomass exports in our
728 study, contrary to our hypothesis relating the trophic state of ponds to exports.
729 Fish presence was only noted as a presence-absence variable and the predation
730 pressure was not evaluated in depth in any of the sampled ponds. Further, neither
731 species information nor stocking densities were considered. All of these factors
732 would be important to understand the impact of fish predation on the
733 macroinvertebrate community (Giles et al. 1995; Tweedy et al. 2013). *Chlorophyll*
734 *a* is widely used as an indicator for the trophic state of aquatic systems, as it can
735 be seen as a proxy for algal biomass which increases with eutrophication.
736 Previously, weak correlations between emerging insect abundances and
737 increasing *chlorophyll a* values have been found (Manning and Sullivan 2021).

738 Recent research has revealed that eutrophication in lakes can limit the availability
739 of LC-PUFA in aquatic food webs (Taipale et al. 2016; Senar et al. 2021). However,
740 we found positive effects of *chlorophyll a*, as a proxy for eutrophication, on PUFA
741 and EPA contents in the emerging insect exports in our study. Usually,
742 eutrophication was linked to a community composition change in phytoplankton,

743 with increasing rates of e.g. Chlorophyta and Cyanobacteria which generally
744 contain less ω 3-PUFA. However, until a certain threshold, eutrophication has been
745 shown to fuel exports of EPA and FA in general (Scharnweber et al. 2020). Further,
746 macroinvertebrate community composition changes have been linked to e.g.
747 macrophyte presence and abundance, rather than nutrient enrichment (Declerck
748 et al. 2011) and would thus present an important explanatory variable. Observed
749 macrophytes have been included as presence-absence data in our data set.
750 However, they have not been considered as main variables in our models because
751 the data was not available for every study pond.

752 Besides temperature effects, further environmental changes could adversely
753 impact the communities inhabiting permanent ponds and thus lead to reductions
754 in the nutrients supplied to the adjacent environments (Jonsson et al. 2015). In
755 lower latitude areas, such as the Mediterranean region, shifts of permanent
756 systems towards temporary or even ephemeral ponds have already been observed
757 (Díaz-Paniagua and Aragonés 2015), which could result in a drastic reduction in
758 fatty acid exports. In ponds with unchanged hydroperiods, the climate change
759 induced changes in environmental parameters (e.g. temperature, conductivity)
760 could also induce alterations in the observed patterns of insect emergence and
761 associated nutrient exports (Jonsson et al. 2015). Given the consumer preference
762 of aquatic prey, besides the direct effect of sustaining consumers diet, emerging
763 aquatic prey can indirectly initiate cascade effects throughout the food web, by
764 leading to increases in the population of predators (e.g. Murakami and Nakano,
765 2002; Dreyer et al. 2016), affecting not only local diversity but also ecosystem
766 functioning (Osakpolor et al. 2023).

767 On a continental scale, the ongoing threats of habitat losses of pond basins due to
768 agricultural drainage and/or climate-induced droughts are expected to continue to
769 reduce emerging insect abundance and furthermore will impact populations of
770 terrestrial consumers (Berzins et al. 2021). Pond management and pond
771 restoration actions are viable options to safeguard higher insect abundances and
772 biomass exports that support a higher abundance and species richness of birds
773 and other riparian consumer species (Lewis-Phillips et al. 2020). The expected
774 variations in environmental parameters induced by global change will inevitably
775 lead to repercussions throughout the entire food web and it is thus crucial to better
776 understand the mechanisms behind insect emergence, to enable better
777 management and protection of those valuable vectors of nutrients.

778

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780

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873 **Conflict of interest**

874 The contributing authors declare no conflict of interest.

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1278 Smith. 2009. Mixed effects models and extensions in ecology with R.
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1283 Table 1. Mixed-ANOVA results for linear mixed effects models (with pond ID as a random
1284 intercept) with biomass export as the response variable and a) spatio-temporal drivers:
1285 season, latitude, altitude and season*latitude and season*altitude interactions, b) most
1286 parsimonious environmental drivers model (based on lowest AIC), with water as a
1287 quadratic term and conductivity as a linear term. See Table S3 in the supplementary
1288 material for model comparisons.

a) Spatio-temporal model with interactions (n=118)					
AIC=	d.f.	<i>F</i> -statistic	<i>p</i> -value	<i>R</i> ² (semi-partial)	<i>R</i> ² (model)
Season	3, 82	29.85	<0.001	0.360	<i>R</i> ² _m =0.502
Latitude	1, 29.4	13.39	0.001	<0.001	<i>R</i> ² _c =0.534
Altitude	1, 35.9	2.11	0.155	<0.001	
Season*Latitude	3, 80.4	6.09	0.001	0.077	
Season*Altitude	3, 83.2	1.07	0.366	0.012	
b) Environmental drivers model (n=90)					

	d.f.	<i>F</i> -statistic	<i>p</i> -value	<i>R</i> ² (semi-partial)	<i>R</i> ² (model)
poly(temperature,2)	1, 82.9	20.14	<0.001	0.276	<i>R</i> ² _m =0.385
chl _a	1, 62.4	0.16	0.693	0.002	<i>R</i> ² _c =0.413
fish	1, 24.2	0.13	0.724	0.003	
conduc	1, 23.4	6.68	0.016	0.037	

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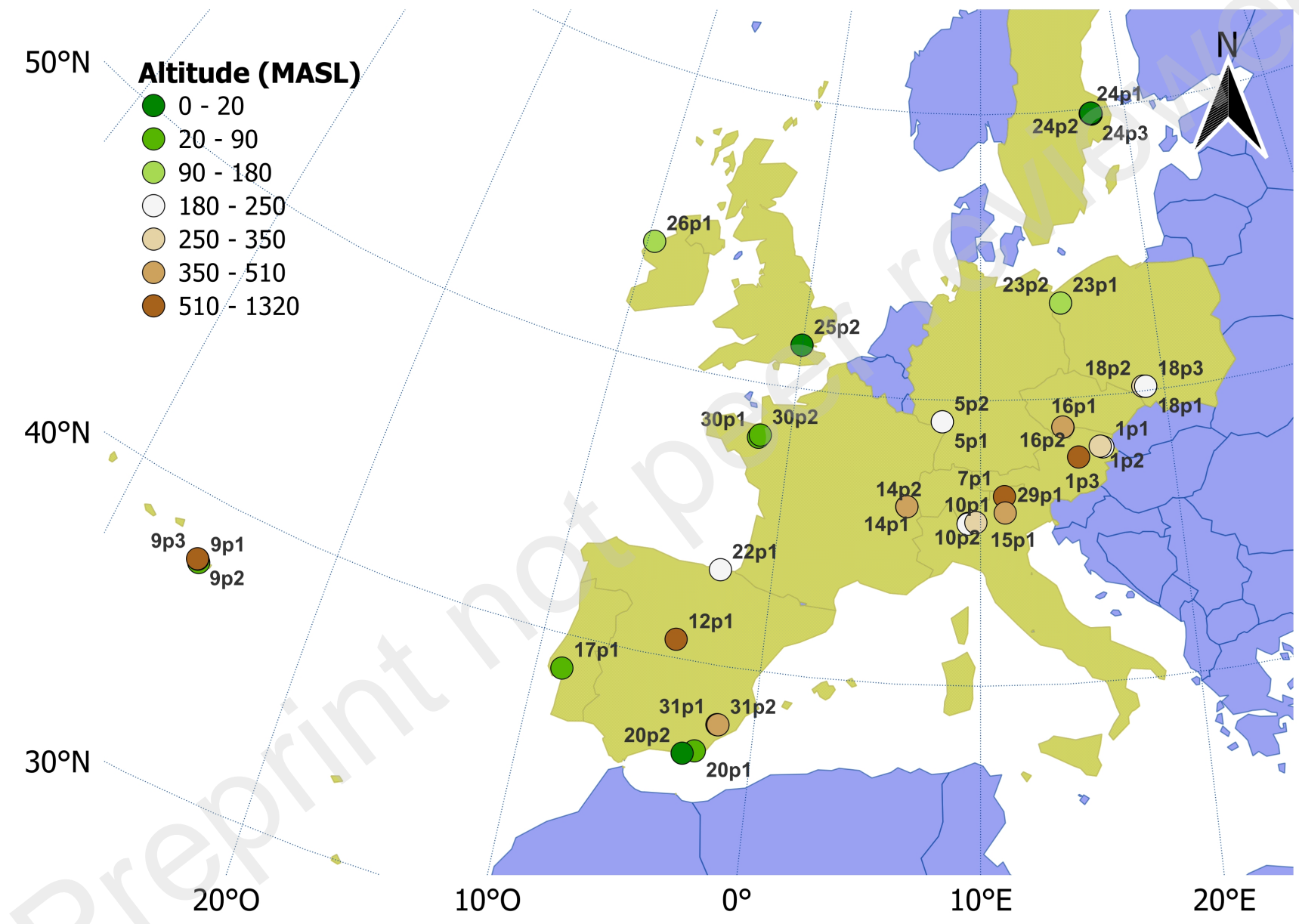
1291 Table 2. Linear mixed effects models predicting export quality (as contents of different
 1292 lipids and ω 3/ ω 6 ratios) based on the taxonomic composition (% biomass) of the main
 1293 recorded taxa (Ephemeroptera, Chaoboridae, Chironomidae, Odonata), environmental
 1294 variables (water temperature, chlorophyll *a*, conductivity) and principal components of
 1295 land use (PC1_urban, PC2_agriculture), with pond ID as a random intercept. For each of
 1296 the variables, the table shows the model estimate and significance ($p < 0.05^*$; $p < 0.01^{**}$,
 1297 $p < 0.001^{***}$), significant values are highlighted in bold. The marginal (*R*²_m) and the
 1298 conditional (*R*²_c) coefficients of determination represent the proportion of the variation
 1299 explained by the
 1300 fixed effects and the whole model, respectively.

	TL (mg/g)	PUFA (mg/g)	ω 3/ ω 6	EPA (mg/g)	DHA (mg/g)
Intercept	4.97***	3.29***	0.17	1.84***	-2.37***
Ephemeroptera	0.12*	0.22***	0.14*	0.28**	-0.01
Chaoboridae	0.07	0.07	0.1	0.16*	0.83***
Chironomidae	-0.05	0.14*	0.03	0.28**	0.32
Odonata	-0.09	0.09	0.17*	0.24**	0.39*
Water temperature	-0.12*	-0.09	-0.05	-0.09	0.16
Chlorophyll <i>a</i>	0.06	0.16**	0.11	0.16*	0.24
Conductivity	-0.07	-0.04	0.12	0.03	0.17

1301

Fish presence	-0.06	-0.26	0.05	0.23	-0.52
Pond size	-0.03	-0.09	-0.03	-0.09	-0.14
PC1_urban	-10 ⁻⁴	-0.03	-0.02	-0.09	0.1
PC2_agriculture	-0.01	-0.10	-0.01	-0.12	-0.06
R^2_m	0.256	0.331	0.191	0.307	0.439
R^2_c	0.646	0.556	0.534	0.427	0.633

1302



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