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RESEARCH ARTICLE

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

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Abstract

Permanent ponds are key landscape units that supply various ecosystem services. Notably, the export of aquatic subsidies to land via emerging insects may significantly influence terrestrial food webs. Polyunsaturated fatty acids (PUFA), which enhance consumer fitness, are among the essential exported components. The patterns and drivers of dietary exports from ponds via insects remain poorly known, particularly at continental scales. We analyzed the exports of biomass, lipid, and fatty acid contents from emerging insects, sampled in 36 ponds across 11 European countries, from 36°N to 59°N and from 26°W to 19°E, over four seasons. We found that biomass and fatty acid exports decreased with increasing latitude and were higher in spring and summer. Seasonal effects also increased with higher latitudes. Temperature was the most important predictor of insect biomass, explaining 27.6% of the total variation and showing an unimodal response. Thus, increasing temperature may promote exports in colder regions and seasons but may negatively influence biomass exports in already warm regions. The exports of total lipids, PUFA, and eicosapentaenoic acid were correlated to exported biomass, while those of docosahexaenoic acid were linked to the emergence of Chaoboridae. Our findings indicated that PUFA contents were affected by taxonomic insect community composition and pond trophic state (indicated by chlorophyll *a*). Two of the correlates identified here (temperature and trophic state) are influenced by anthropogenic activity via climate and land use change, respectively. Thus, human activity impacts the food webs in and around ponds by influencing the quantity and quality of nutritional exports.

Organic matter and nutrient fluxes across space are important for ecosystem functioning (Barnes et al. 2018), with vectors ranging from desert dust (Prospero et al. 2020) to emerging insects (Martin-Creuzburg et al. 2017). Reciprocal subsidies are critical for both terrestrial and aquatic food webs (Nakano and Murakami 2001); but exports from small water bodies, such as ponds, have largely been overlooked (Fehlinger et al. 2023a). This limits our understanding of the impacts of pond ecosystems on the surrounding landscape (but *see* Lewis-Phillips et al. 2020; Fehlinger et al. 2023b).

Ponds, that is, small shallow water bodies (< 5 ha, < 5 m depth) with less than 30% emergent vegetation (Richardson et al. 2022), are key ecological landscape components, supporting biodiversity, providing valuable ecosystem services (Hill et al. 2021), and producing large quantities of insect biomass (Dalal and Gupta 2016; Fehlinger et al. 2023b) contribute significantly to the diets of many terrestrial consumers, such as birds (25%–100%; Baxter et al. 2005; Bartels et al. 2012), bats (Frank et al. 2012), or spiders (Fritz et al. 2017).

Aquatic subsidies generally provide higher nutritional quality, energy density, and nutrient concentration than terrestrial ones, despite often being lower in quantity (Bartels et al. 2012; Twining et al. 2019; but *see* Twining et al. 2025). This is largely due to the prevalence of key biomolecules, such as long-chain polyunsaturated fatty acids (LC-PUFAs) in aquatic organisms (Napolitano 1999; Hixson et al. 2015). Long-chain polyunsaturated fatty acids are essential compounds that support the overall fitness and immune function of consumers (Brett and Müller-Navarra 1997; Fritz et al. 2017). Omega-3 (ω3) LC-PUFAs, such as docosahexaenoic acid (DHA) or eicosapentaenoic acid (EPA), and arachidonic acid (ARA; an omega-6 [ω6] LC-PUFA) are particularly important for brain function and size (Závorka et al. 2022), inflammatory responses (Tocher 2003) and metabolism (Pilecky et al. 2021). These biomolecules are primarily produced by microalgae (Napolitano 1999). Aquatic insects, like most metazoans, cannot synthesize LC-PUFAs de novo and rely on dietary uptake (Malcicka et al. 2018; Gladyshev et al. 2013).

While the quantity of PUFA export mainly depends on insect biomass (e.g., Scharnweber et al. 2020; Fehlinger et al. 2023b), the PUFA composition varies with taxonomic composition (Parmar et al. 2022) due to differences in feeding strategy and/or fatty acid (FA) metabolism (Guo et al. 2018). Among aquatic insects, Ephemeroptera and Chaoboridae have high nutritional quality as they contain particularly high levels of EPA and DHA, respectively, compared to other common taxa such as Chironomidae and Trichoptera (Parmar et al. 2022; Martin-Creuzburg et al. 2017). Therefore, factors shaping aquatic insect community structure, such as predator presence, resource availability, water chemistry, and waterbody morphology (Biggs et al. 2005; Cereghino et al. 2008; Becerra Jurado et al. 2009), are also expected to affect PUFA contents in aquatic insect exports.

Environmental factors, such as nutrient loading, temperature, and land use, also affect PUFA content within aquatic insect taxa and influence transfers to terrestrial ecosystems (Nash et al. 2023; Scharnweber et al. 2020). For instance, eutrophication could reduce Omega-3 LC-PUFA transfer in food webs due to increasing dominance of low-quality algae and cyanobacteria (Taipale et al. 2016; Müller-Navarra et al. 2000). Furthermore, increasing temperatures might reduce PUFA content in aquatic insects, as with other ectotherms, due to homeoviscous adaptation (Hixson and Arts 2016; Holm

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et al. 2022). Temperature is also a key driver of insect phenology (e.g., Bonacina et al. 2023), where climate change is driving timing mismatches between emerging insects and insectivorous birds (Shipley et al. 2022). Additionally, different forms and intensities of land use can affect PUFA export to adjacent terrestrial ecosystems by driving spatiotemporal variation in community composition and phenology (Ohler et al. 2024), and influencing cross-system food web dynamics. For example, intensified agriculture has been linked to increasing trophic state of ponds (Usio et al. 2017), and increased eutrophication and browning can limit LC-PUFA availability in aquatic food webs by causing shifts in phytoplankton communities and trophic interactions (Müller-Navarra et al. 2000; Taipale et al. 2016; Senar et al. 2021). Gaining further insights into the amounts and quality of PUFAs exported via emerging insects and the variations of exports along spatial, seasonal, and land-use gradients is crucial to gauge the stability of this high-quality resource for terrestrial ecosystems.

We aimed to advance the understanding of the spatio-seasonal variation in PUFA and insect biomass exports from permanent ponds across Europe, along a broad latitudinal and longitudinal gradient, ranging from 36°N to 59°N and from 26°W to 19°E. We quantified emerging insect biomass exports and analyzed their total lipid and specific FA content.

We hypothesized that (i) temperature will drive biomass export, with higher exports in warmer seasons and at lower latitudes; (ii) trophic state will affect the quantity and quality of exports, leading to increased biomass and FA exports with higher productivity, but resulting in lower LC-PUFA content per unit of biomass due to reduced algal quality. Trophic state is also related to land use (Usio et al. 2017) which is expected to impact the quantity and quality of FA exports, since we expect distinct communities in ponds in near-natural compared to urbanized environments. We expect higher emerging biomass in urban and agricultural surroundings, associated with nutrient pollution, and less in forested areas. In contrast, we expect a lower PUFA content in emerging insects from agricultural and urban contexts than forested and open natural areas, due to expected differences in basal resource quality; and (iii) we hypothesize that taxonomic composition is a key driver of FA

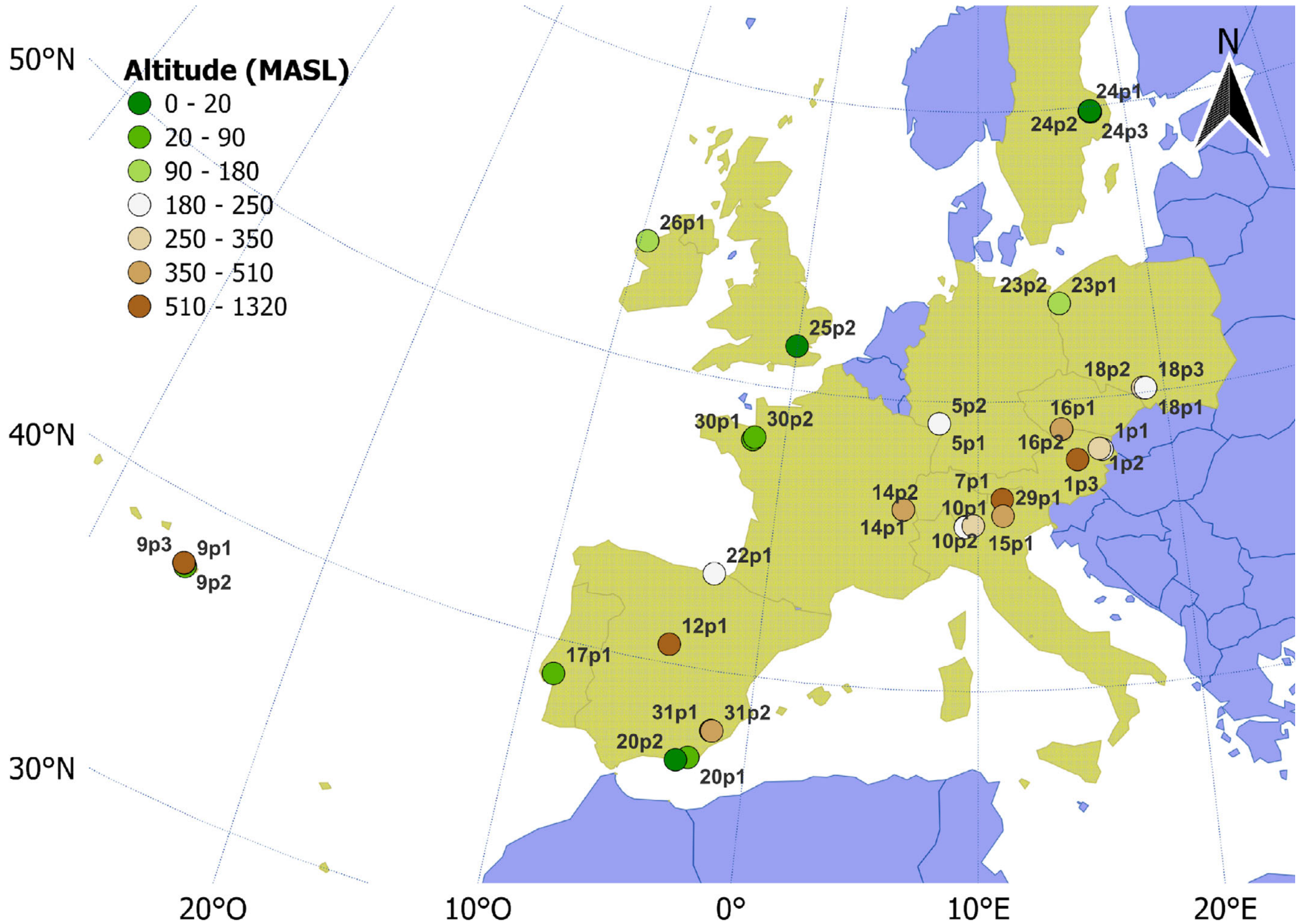

Fig. 1. Distribution of the study ponds ($n = 36$), dot color corresponds to altitude, Pond IDs consist of team number, p for pond, number of sampled ponds per team selected for field work across 11 different European countries (studied countries are green). Altitude is in meters above sea level (MASL).

composition of aquatic insect exports, where the abundance of key taxa disproportionately affects the exports to land.

Materials and methods

Study sites and land use categorization

Our studied sites included 36 ponds across 11 European countries (Fig. 1), covering a wide range, from southern Spain to Sweden and from the Azores to Poland. The climatic conditions show considerable variability, from a Mediterranean climate in the south with hot summers and mild, wet winters to a temperate climate in the north with cooler temperatures and more rainfall, influenced by the Atlantic Ocean in the western part. The eastern countries have a more continental climate with cold, snowy winters and warm summers.

In each country, one to seven ponds were chosen for sampling on the basis of water permanence, depth, and accessibility, with all ponds permanently flooded and with a maximum depth of 3 m (Supporting Information Tables S1, S2). The ponds were mostly of artificial origin, different ages, and were located at different altitudes (Supporting Information Tables S1, S2; Fig. 1). Observations confirmed fish in two thirds of the studied ponds (Supporting Information Tables S1, S2). Land use in the pond-adjacent area ranged from fully forested to entirely agricultural or urban (Supporting Information Fig. S1; Supporting Information Table S2), based on the Corine Land Cover (CLC) 2018 database (scale 1:100.000; EEA 2018) within a 100 and 1000 m buffer (radius) from the pond centroid (Thornhill et al. 2017). A detailed description of the reclassification of CLC categories and the PCA used to summarize gradients is available in the Supporting Information Methods.

Emerging insects sampling

We sampled from autumn 2020 to summer 2021 once in each season ($n = 4$ seasons). Aquatic emerging insects were collected twice within 1 week at 3-d intervals and then pooled, reflecting the cumulative insect emergence over 6 d. Emerging insects were caught using pyramid-shaped floating emergence traps, consisting of a net ($\sim 500\ \mu$m) fixed to a PVC-pipe structure and crowned by an external collection bottle (Supporting Information Fig. S2; Cadmus et al. 2016). To maximize the representativeness of insect samples, emergence traps were intentionally deployed to cover all potential pond habitats, with one to three traps covering a total surface of 0.54 to 3 m^2. The traps were manually emptied on Days 3 and 7 after deployment to ensure that samples were not too degraded for biochemical analysis. Upon arrival in the laboratory, samples were frozen (at or below -20°C) and freeze-dried for analysis. The emerging insects were identified under stereo-microscopes using national or regional-level identification keys to the lowest possible taxonomic level and then unified to Order level prior to analysis for consistency (literature selection in Supporting Information). Orders contributing < 5% biomass were grouped together as "Others" (Supporting Information Table S3). From the maximum 144 samples that could potentially be obtained from 36 ponds, we were able to measure aquatic insect biomass from 118 samples including frozen ponds that were assigned a 0 emergence (Supporting Information Table S4). Of these samples, we were able to analyze lipid and FA exports from 101 and FA contents from 89 sites after excluding the 12 ponds that were frozen (Supporting Information Table S4).

Environmental data collection and parameter selection

During each sampling event, conductivity, oxygen saturation, pH, water temperature, and transparency (Secchi depth) were measured. Additionally, visual assessments of substrate heterogeneity were conducted, and the percentage of surface covered by submerged and emergent macrophytes was recorded (Supporting Information Table S2). Weather data was recorded for the sampling day and three preceding days, and fish presence was noted at each site (Supporting Information Tables S1, S2). Chlorophyll *a* (Chl *a*) concentration was measured either in situ or in the lab. Temperature, Chl *a*, conductivity, and fish presence were retained in the analyses as the most likely bottom-up and top-down drivers of insect abundance with the least missing values combined (Supporting Information Table S2).

Fatty acids analysis and sample selection

Fatty acids were extracted from 280 taxon-specific samples across 89 pond-season combinations (Supporting Information Tables S3, S4) following Heissenberger et al. (2010), described here briefly and detailed in Supporting Information Methods. Total lipid (TL) extracts were weighed before and after evaporation, and a portion was trans-methylated and analyzed by gas chromatography. Some samples had insufficient mass for analysis (< 2 mg dry weight [DW]). To prevent the removal of these ponds, we extrapolated the TL and FA content of those samples from the TL and FA means in the entire dataset. This is based on the assumption that the majority of FA export variability is driven by differences in quantities of biomass exported (Martin-Creuzburg et al. 2017; Scharnweber et al. 2020). The extrapolation affected 33 samples, where the mean contribution of the extrapolated amounts per sample was $2.9 \pm 2.4\%$ of the TL exports and less than 1% for the different FA exports, which is much lower than the spatio-seasonal variation in lipid and FA exports (Supporting Information Table S5; means and SD). By accepting this low extrapolation error, we avoided the reduction of 37% of our data points for statistical analysis.

Biomass and export quality calculations

The omega-3/omega-6 PUFA ratio (ω3/ω6) was used as a proxy for the quality of FA composition. The biomass export rate ($\mathrm{mg\,m^{-2}\,d^{-1}}$) from each pond during a specific season was calculated according to Eq. 1. The ratio of lipids in exports, that is, lipid content ($\mathrm{mg\,g^{-1}}$ biomass), was calculated according to Eq. 2, and the percentage contribution of individual lipids and FAs was calculated as detailed in Eq. 3.

$$\text{Biomass export rate} = \text{DW in mg}/\left(\text{area sampled in m}^2 \times \text{number of days}\right), \left(\mathrm{mg\,m^{-2}\,d^{-1}}\right) \quad (1)$$

$$\text{Lipid content} = \text{lipid mass in mg}/\text{biomass in g of DW}, \left(\mathrm{mg\,g^{-1}\,DW}\right) \quad (2)$$

$$\text{Taxon} \times \text{Lipid/FA contribution}\,(\%) = \text{lipid/FA} \times \text{export}\left(\mathrm{mg\,m^{-2}\,d^{-1}}\right) / \text{total lipid export}\left(\mathrm{mg\,m^{-2}\,d^{-1}}\right) \times 100 \quad (3)$$

Exports ($\mathrm{mg\,m^{-2}\,d^{-1}}$) and contents ($\mathrm{mg\,g^{-1}}$ DW) were $\log_{10}(x)$ transformed; for export variables including zeroes, we used a $\log_{10}(x + 0.1^i)$-transformation i, where i was chosen based on the order of magnitude of each variable: biomass export ($i = 1$), TL export ($i = 2$), PUFA export ($i = 4$), EPA export ($i = 4$), DHA export ($i = 5$), DHA content ($i = 2$). All numerical explanatory variables were standardized by centering them around the mean and dividing them by their standard deviation, that is, z-scores. For statistical analyses, the following response variables were used: biomass ($\mathrm{mg\,m^{-2}\,d^{-1}}$, *see* Eq. 1), total FAs (TFA, *see* Eq. 2), and total lipids (TL, *see* Eq. 3) per pond and per sampling season. In addition, we investigated the drivers for specific FAs (e.g., EPA) and total PUFA in $\mathrm{mg\,g^{-1}}$.

Statistical analysis of export drivers

To test the effects of spatial, seasonal, and environmental drivers on biomass and FA export quantities, linear mixed effect models (LMM) were fitted (restricted maximum likelihood), with pond ID as a random factor. Fixed effects included spatial (latitude, elevation) and seasonal gradients based on 118 data points from 36 ponds: latitude, season, Chl *a*, temperature, fish presence, land use (exported PCA axes), and pond size (*see* Supporting Information Methods for full model structure). Highly correlated variables (Supporting Information Fig. S3) were excluded, and interaction terms were tested (Supporting Information Methods). The non-linear responses of biomass exports to environmental drivers (i.e., temperature, Chl *a*, and land use, as summarized by the PCA axes) were assessed by using LMMs with quadratic terms (Supporting Information Table S6 for model equations and results; Supporting Information Methods).

Models were selected following the AIC criterion, whereby $\Delta\mathrm{AIC} < 2$ indicates "substantial" support (Burnham and Anderson 2002), and the contributions of variables were assessed by calculating semi-partial R^2 estimates. Residual diagnostics and multicollinearity were checked to ensure model assumptions were met (Supporting Information Methods). Additionally, we tested the predictive power of biomass on lipid and FA exports by running linear regressions fitted by ordinary least squares (OLS), with biomass export as a predictor of TL, PUFA, EPA, and DHA ($n = 89$), and Chaoboridae biomass as a predictor of DHA exports (Supporting Information Methods), and by inspecting the coefficient of determination (R^2).

We defined the nutritional quality of export as the contents of lipids, PUFA, EPA, and DHA per unit of exported biomass ($\mathrm{mg\,g^{-1}}$ DW) and as the ω3/ω6 PUFA ratios. To test for taxonomic differences, we used LMMs with taxon group as a fixed effect, followed by post-hoc tests for pairwise comparisons (Supporting Information Methods). Further, we investigated FA export quality variations using redundancy analysis (RDA) based on total biomass and environmental predictors (water temperature, fish presence, pond size, conductivity, Chl *a*, and the first two principal components of land use ($n = 74$)). Finally, we used LMMs to assess the effects of taxonomic and environmental drivers on the quality of exports (Supporting Information Methods). All statistical analyses were carried out in R (R Core Team 2022).

Results

Biomass, total lipid, and fatty acid exports

Biomass exports via emerging insects were variable among ponds across Europe (Supporting Information Table S7) and within ponds across seasons (Supporting Information Table S5). They ranged from 0 mg DW $\mathrm{m^{-2}\,d^{-1}}$ in autumn and winter at high latitudes, where many ponds were frozen, to 208.2 mg DW $\mathrm{m^{-2}\,d^{-1}}$ in a productive pond during summer (Supporting Information Table S7). Lipids accounted for on average 14.9% (± 6.2 SD) of the biomass exports, whereas PUFAs represented 2.63% (± 1.3 SD) (Supporting Information Table S8). Exports of EPA reached up to 2.95 mg DW $\mathrm{m^{-2}\,d^{-1}}$, while DHA exports were more than one magnitude lower (Supporting Information Table S7) and below detection limits in 15 of the 89 pond-per-season samples used for FA analysis. On average, ω3 exports from our ponds were higher than ω6 exports (ω3/ω6 > 1; Supporting Information Table S7), and the ω3/ω6 ratio varied greatly among ponds (range 0.6–2.6), but not among seasons (Supporting Information Tables S7, S8).

Drivers of export quantity

Spatial and seasonal predictors (latitude, altitude and season) explained 50.2% of biomass export variation (R^2_{m}), with significant effects of season and latitude but not of altitude (Table 1a). Season explained the vast majority of the biomass

Table 1. Results of the mixed-ANOVA run for linear mixed effects models. Pond ID was used as a random intercept, and biomass export was the tested response variable.

(a) Spatio-temporal model with interactions ($n = 118$)

AIC =	d.f.	*F*-statistic	*p*-value	R^2 (semi-partial)	R^2 (model)
Season	3, 82	29.85	< 0.001	0.360	$R^2_m = 0.502$
Latitude	1, 29.4	13.39	0.001	< 0.001	$R^2_c = 0.534$
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.	*F*-statistic	*p*-value	R^2 (semi-partial)	R^2 (model)
Water temperature ($x + x^2$)	1, 82.9	20.14	< 0.001	0.276	$R^2_m = 0.385$
Chlorophyll *a*	1, 62.4	0.16	0.693	0.002	$R^2_c = 0.413$
Fish presence	1, 24.2	0.13	0.724	0.003	
Conductivity	1, 23.4	6.68	0.016	0.037	

exports (36.0%, semi-partial R^2; Table 1a), showing higher exports in spring and summer (Tukey HSD in model without interactions, $p < 0.001$, Fig. 2a). Latitude had an overall negative effect on biomass exports (Table 1a; Fig. 2b). However, the effect of latitude was dependent on season (significant season: latitude interaction; Table 1a) with steeper slopes in winter than in spring ($\Delta_{\text{Winter–Spring}} = -0.15 \pm 0.06$, $p = 0.046$) and summer ($\Delta_{\text{Winter–Summer}} = -0.24 \pm 0.06$, $p < 0.001$). Note that there are more zero values in winter since many ponds were frozen (Fig. 2a, b; Supporting Information Table S7). This season: latitude interaction term explained 7.7% of the variation in biomass exports (semi-partial R^2; Table 1a). Single linear models per season showed decreases in biomass exports with latitude in winter (slope $= -0.18 \pm 0.04$, $F_{1,28} = 23.8$, $p < 0.001$, $R^2 = 0.46$) and autumn (slope $= -0.11 \pm 0.04$, $F_{1,24} = 6.3$, $p = 0.016$, $R^2 = 0.21$), while no significant trends were found in spring (slope $= -0.05 \pm 0.04$, $F_{1,31} = 1.8$, $p = 0.18$, $R^2 = 0.06$) or summer ($F_{1,27} = 0.8$, $p = 0.38$, $R^2 = 0.03$).

In the study of the environmental drivers of the biomass exports, the model including bottom-up drivers (water temperature, Chl *a*), top-down drivers (fish presence), and water chemistry (i.e., conductivity) was the best fit model (Supporting Information Table S6). Water temperature explained most of the variation (27.6%; semi-partial R^2; Table 1b) and had a significant quadratic relationship ($R^2_m = 0.385$, $p < 0.001$; Fig. 2c; Table 1b). Neither Chl *a*, as a proxy for trophic status, nor fish presence significantly affected the biomass exports (Table 1b). Conductivity, on the other hand, had a significant positive effect on biomass exports (Fig. 2d), explaining 3.7% of the variability (semi-partial R^2; $p < 0.05$; Table 1b).

Biomass significantly explained the majority in emerging insect exports variation of TL, PUFA, and EPA per sampling, and was a highly significant predictor for DHA exports ($p < 0.001$; Supporting Information Table S9). However, the predictive power of biomass to DHA export was lower than other lipid exports investigated ($R^2 = 0.66$; Supporting Information Table S9). Including Chaoboridae biomass in the regression model increased the goodness of fit of the model by 10% ($R^2 = 0.76$, intercept $= -7.87 \pm 0.30$, slope$_{\text{biomass}} = 0.84 \pm 0.06$, slope$_{\text{Chaoboridae}} = 0.83 \pm 0.12$, $p < 0.001$). When Chaoboridae were present, Chaoboridae biomass export predicted 82% of the variation in pond DHA exports ($R^2 = 0.82$, intercept $= 5.62 \pm 0.26$, slope $= 1.15 \pm 0.16$).

Taxon-specific contributions to fatty acid exports

Lipids and FAs content differed significantly among taxa (Fig. 3; Supporting Information Fig. S4; Supporting Information Table S10). Ephemeroptera contributed the most to TL (41.1%), PUFA (42.7%), omega-3 (45.2%), omega-6 (39.1%) and EPA (33.7%) exports, despite contributing less to exported biomass (19.5%, Fig. 3; Supporting Information Table S3). On the other hand, Chironomidae had a high contribution to biomass exports (48.1%), but lower contributions to TL exports (13%–32%, Fig. 3; Supporting Information Fig. S4). Docosahexaenoic acid exports were highly dependent on Chaoboridae midges (57.2%) despite lower biomass contribution (4.9%; Fig. 3). Other taxa contributing > 10% of the DHA exports were Ephemeroptera (21.3%) and Chironomidae (13.7%) (Fig. 3). Note that the high contribution of Ephemeroptera to DHA export is only based on one sample (Fig. 3).

Drivers of export quality

Environmental variables (water temperature, fish presence, pond size, Chl *a*, conductivity and land use) explained 14.7% of the variation in the community composition (RDA; Supporting Information Table S11). Only water temperature significantly contributed to the RDA model (Fig. 4;

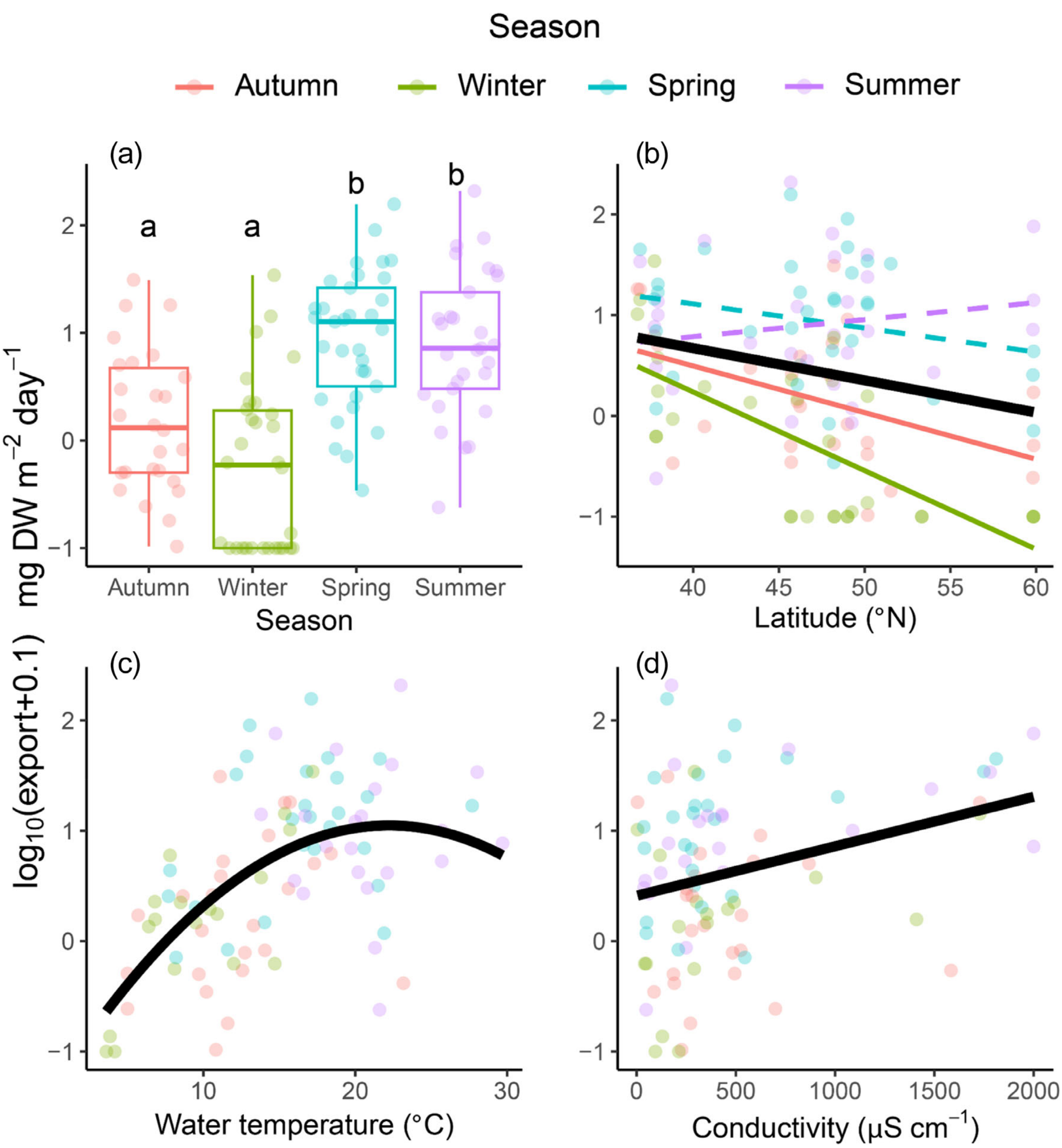

Fig. 2. Effect of (**a**) season, (**b**) latitude, (**c**) water temperature, and (**d**) conductivity on biomass export. In (a), different letters indicate significant seasonal differences ($p < 0.05$); boxes depict median, 25th and 75th percentile, and whiskers extend to maximum and minimum values. In (b), the thick, black line represents the overall effect of latitude. Solid lines are significant ($p < 0.05$) and dashed lines show non-significant trends. For (a) and (b), $n = 118$; for (c) and (d), $n = 90$.

Supporting Information Table S11) and explained 4.58% of the variation, while the proxies for urbanization and agricultural land use were marginally significant (Supporting Information Table S11). Agricultural and urban land use proxies were positively correlated with the relative biomass of Chironomidae. Likewise, forest land use, denoted by a negative PC1_urban, was correlated to the occurrence of Chaoboridae and "Others" (Fig. 4; Supporting Information Table S11).

In our analysis for main drivers of lipid and FA contents in the emergence (as mg g^{-1} biomass), we found that TL contents and PUFAs were positively associated with a higher relative biomass of Ephemeroptera in the emerging insect community. For EPA, we found positive effects of the contribution of Ephemeroptera, Chaoboridae, and Odonata, which were high in EPA contents (Table 2; Fig. 3; Supporting Information Fig. S4). The models also suggested a significant positive effect of Chironomidae contribution, even though this taxon generally did not have high EPA contents (Table 2; Fig. 3; Supporting Information Fig. S4). Further, ω3/ω6 ratios of the exports were positively affected by the dominance of Ephemeroptera and Odonata (Table 2), while most of the DHA contents were

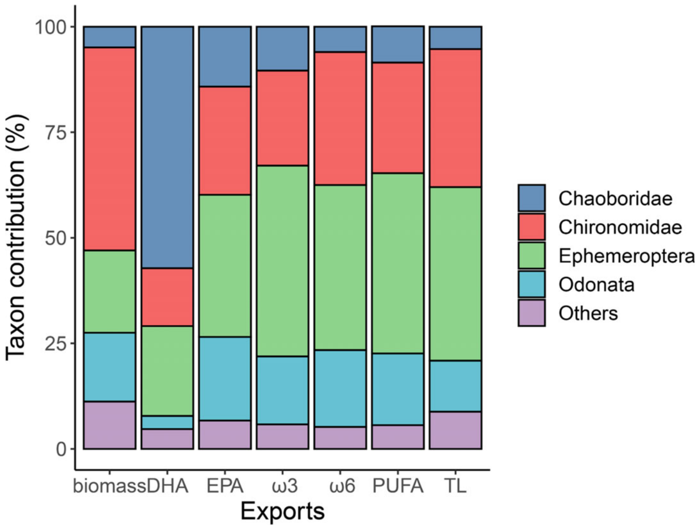

Fig. 3. Percent taxonomic contribution to the different types of exports, where "Others" are the pooled taxa that individually contributed less than 5%. ω3 = omega-3, ω6 = omega-6.

positively related to the relative Chaoboridae biomass (Fig. 3; Supporting Information Fig. S4). After accounting for the effects of taxonomic composition, we also found significant effects of environmental drivers (such as Chl *a*) on PUFA and EPA contents of the exported biomass (Table 2).

Discussion

Our study represents the first comprehensive investigation at a continental scale of the quantity and quality of emerging insect exports, considering both spatial and seasonal dynamics. Overall, it highlights the importance of climate and community composition in driving aquatic insect lipid exports to land. As hypothesized, insect biomass exports increased with temperature and decreased with latitude across Europe, confirming global emergence patterns associated with latitude and climate (Nash et al. 2023); and local patterns connecting emergence and water temperatures (Lewis-Phillips et al. 2020). Yet, the unimodal response of emergence to water temperature suggests non-linear temperature responses: Colder regions and seasons may benefit from warming conditions, while warmer regions and seasons may be negatively affected by temperatures past the 20°C optima on to the 25°C threshold (Fig. 2c). Unlike hypothesized, higher Chl *a*, as a proxy for algal biomass, did not significantly impact insect biomass, FA quantity, or quality. Instead, community composition played a larger role for specific FA exports, particularly the occurrence of LC-PUFA-rich taxa such as Ephemeroptera and Chaoboridae. This taxonomic dependency highlights the importance of insect community composition in delivering nutrients from permanent ponds to the terrestrial environment across Europe.

Spatio-seasonal patterns in aquatic insect exports

Overall, the highest biomass exports occurred in spring and summer, in line with previous studies (Nakano and Murakami 2001; Uesugi and Murakami 2007). Our biomass exports in summer (21.6 ± 45.7 mg DW m^{-2} d^{-1}) are comparable to those reported from eutrophic fish ponds in Austria and from managed farm ponds in the UK in the same season (~ 13.6 mg DW m^{-2} d^{-1}, Fehlinger et al. 2023b, and 52 mg DW m^{-2} d^{-1}, Lewis-Phillips et al. 2020, respectively). They are also comparable in magnitude to exports from lakes or rivers (Gratton and VanderZanden 2009; Bartels et al. 2012). It is important to note that our sampling campaigns were not timed to capture emergence peaks, so we likely underestimated the exported biomass and FAs in our dataset. These peaks could in the future be monitored using novel technologies implementing remote sensing and automated insect detection and identification, which would help follow the developments of emergence peaks, particularly in times of climate change where such temperature-controlled events are expected to change (e.g., Roy et al. 2024; Shipley et al. 2022).

Interestingly, the effect of season varied with latitude, with increasing seasonal export variation at higher latitudes, in line with results from a global emergence meta-analysis, and potentially related to seasonality in temperature and precipitation (Nash et al. 2023). In our dataset, pronounced seasonality at higher latitudes was caused by frozen ponds in winter, for example, in Sweden or the Czech Republic. Emerging aquatic insects can enter diapause during the ice-cover period of ponds to optimize emergence timing for reproduction (Lencioni 2004). Such differences in the seasonality within the continent can have important ecological implications for terrestrial consumers, because aquatic insects are a temporary high-quality resource (Twining et al. 2019; Parmar et al. 2022). Therefore, climate change-induced decoupling between the timing of emergence and the demand of terrestrial consumers could lead to negative consequences throughout the entire food web (Shipley et al. 2022).

Taxonomic contributions to fatty acid exports

Almost 50% of exports in our entire dataset were made up of Chironomidae, similar to other freshwater systems (Baxter et al. 2005; Martin-Creuzburg et al. 2017). While Ephemeroptera (~ 20%), Odonata (~ 16%) and Chaoboridae (~ 5%) made up smaller portions of the total biomass exported, their contributions to the overall FA exported were considerable, particularly regarding DHA exports, which were mainly explained by Chaoboridae biomass. In general, Ephemeroptera and Chaoboridae contained the most EPA and omega-3 PUFA, highlighting the importance of diverse communities for the export of dietary nutrients (Shipley et al. 2024) and emphasizing the ecological role of different taxa in terms of their FA profiles (Parmar et al. 2022). Still, a large fraction of lipid and FA analyzed was predicted by biomass. Thus, the effect of quality (i.e., community composition and FA composition) on

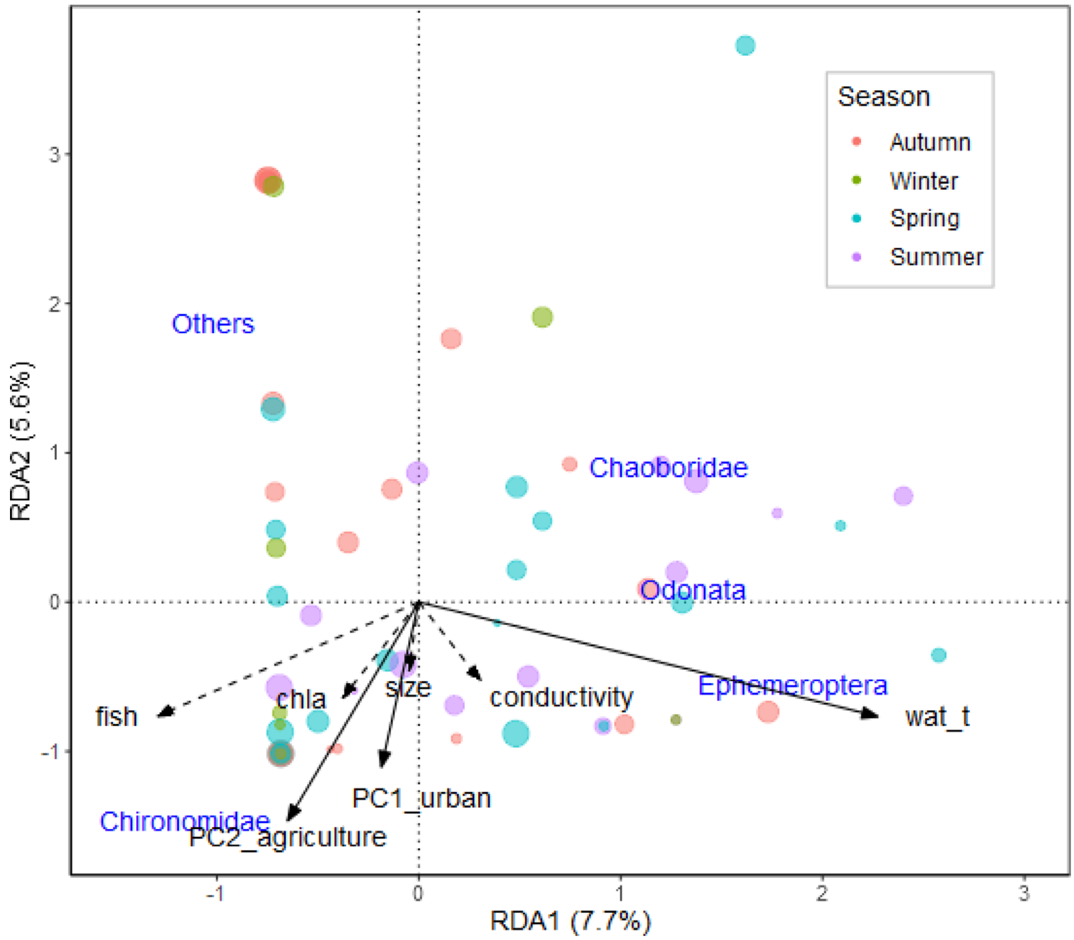

Fig. 4. Redundancy analysis of the insect community composition in response to environmental drivers ($n = 74$). Blue names are insect taxa eigenvectors. Symbol size is directly proportional to latitude. Black arrows and names are eigenvectors of environmental variables included in the model, where solid arrows represent significant predictors; $p < 0.05$. wat_t = water temperature, chla = chlorophyll *a*, fish = fish presence, PC1_urban = proxy for urbanization, PC2_agriculture = proxy for agricultural land use, size = pond size.

FA and lipid exports is smaller compared with the effect of quantity (i.e., emerging biomass).

Environmental drivers of biomass and fatty acid exports

Contrary to our hypothesis relating the trophic state of ponds to exports, neither Chl *a* nor fish presence seemed to impact biomass exports in our study. This contrasts with the strong negative effects of fish presence and the overall positive effects of nutrient levels on biomass and FA exports by aquatic insects in experimental mesocosms (Scharnweber et al. 2020). It might suggest that the effects of those factors are weaker in complex real-world ecosystems than in a controlled environment; however, the absence of detailed data on fish communities calls for caution in interpreting their impact (Tweedy et al. 2013). Further, while Chl *a* is a widely used proxy for productivity, it strongly fluctuates throughout seasons, and reliable relations between nutrient concentrations and Chl *a* might only be deductible from long-term observations (Davidson et al. 2023). We were not able to measure nutrient levels directly, but as electric conductivity can be driven by dissolved nutrient ions, the positive effect of conductivity on emergence may have reflected the expected effect of trophic state (Mamun 2025).

With regards to the effect of environmental drivers on export quality (i.e., lipid contents mg g^{-1}), we found positive effects of Chl *a* on PUFA and EPA contents in aquatic insect exports. We did not find any direct effects of land use on lipid or FA contents in exports, opposite to our second hypothesis. Eutrophication has been linked to limited LC-PUFA in aquatic food webs (Taipale et al. 2016; Senar et al. 2021) and lower ω3-PUFA due to phytoplankton community shifts (Müller-Navarra et al. 2000), while land use has been known to affect PUFA exports (Ohler et al. 2024). Such discrepancies may arise from our analysis controlling for other variables, meaning that eutrophication and land use effects may be indirect through other drivers, such as community composition. Similarly, we found no direct effect of temperature on PUFA, suggesting that the effects of homeoviscous adaptation cannot be

Table 2. Linear mixed effects models predicting export quality (as contents of different lipids and ω3/ω6 ratios) based on taxonomic composition (% biomass) of main taxa (Ephemeroptera, Chaoboridae, Chironomidae, Odonata), environmental variables (water temperature, chlorophyll *a*, conductivity) and principal components of land use (PC1_urban, PC2_agriculture), with pond ID as a random intercept. For each of the variables, the table shows the model estimate and significance ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***), significant values are highlighted in bold. The marginal (R^2_m) and the conditional (R^2_c) coefficients of determination represent the proportion of the variation explained by the fixed effects and the whole model, respectively.

	Intercept	Ephemeroptera	Chaoboridae	Chironomidae	Odonata	Water temperature	Chlorophyll-a	Conductivity	Fish presence	Pond size	PC1_ urban	PC2_ agriculture	R^2_m	R^2_c
TL (mg g^{-1})	4.97***	0.12*	0.07	−0.05	−0.09	−0.12*	0.06	−0.07	−0.06	−0.03	-10^{-4}	−0.01	0.256	0.646
PUFA (mg g^{-1})	3.29***	0.22***	0.07	0.14*	0.09	−0.09	0.16**	−0.04	−0.26	−0.09	−0.03	−0.10	0.331	0.556
ω3/ω6	0.17	0.14*	0.1	0.03	0.17*	−0.05	0.11	0.12	0.05	−0.03	−0.02	−0.01	0.191	0.534
EPA (mg g^{-1})	1.84***	0.28**	0.16*	0.28**	0.24**	−0.09	0.16*	0.03	0.23	−0.09	−0.09	−0.12	0.307	0.427
DHA (mg g^{-1})	−2.37***	−0.01	0.83***	0.32	0.39*	0.16	0.24	0.17	−0.52	−0.14	0.1	−0.06	0.439	0.633

detected at these taxonomic and geographical scales. Further investigations are necessary to better understand the direct environmental drivers of lipid contents of insect exports at large scales.

Anthropogenic impact on biomass and fatty acid exports from ponds

On a continental scale, the ongoing pond habitat losses due to agricultural drainage and/or climate-induced droughts are expected to continue, further reducing emerging insect abundance and impacting terrestrial consumers (Berzins et al. 2021; Jonsson et al. 2015). Climate change is amplifying multiple stressors on ponds due to their greater vulnerability compared to larger water bodies, for example, changes in rainfall, conductivity, land use, and temperature fluctuations (Díaz-Paniagua and Aragonés 2015; Jonsson et al. 2015). Together, those could result in a drastic reduction in FA exports. We found a positive influence of conductivity on biomass exports, which had previously been linked to increased agriculture, thus connecting land use and water conductivity levels (Kupiec et al. 2021). While we did not find a direct influence of land use on the FA exports, we found a positive correlation between increasing agriculture, urbanization, and Chironomidae biomass, similar to Ohler et al. (2024). Given the links between land use changes, climate, and community composition of aquatic insects, the vulnerability of these essential resources becomes evident. Qualitative and quantitative changes in emerging aquatic prey can initiate cascade effects throughout the terrestrial food web, affecting local diversity but also ecosystem functioning (Murakami and Nakano 2002; Dreyer et al. 2016; Osakpolor et al. 2023). Pond management, creation, and restoration actions are viable options to safeguard higher insect biomass exports that support a higher abundance and species richness of birds and other riparian consumer species (Lewis-Phillips et al. 2020).

Conclusion

Overall, this study highlights the pivotal role of ponds in distributing essential resources across a broad geographical scale, thereby emphasizing their significance as fundamental ecosystems within the landscape. The strong influence of temperature on export quantity suggests that these exports are highly susceptible to rising temperature and increasing temperature fluctuations (i.e., heat waves, cold waves), which are in line with climate change predictions (IPCC 2023). Furthermore, the effects of insect community composition on the nutritional quality of the emergence suggest that the preservation of key taxa in ponds, such as Chaoboridae and Ephemeroptera, is key to providing high-quality Omega-3 LC-PUFA to terrestrial consumers. Therefore, our study highlights the importance of preserving aquatic insect biodiversity to have high-quality exports to terrestrial ecosystems.

Author Contributions

Lena Fehlinger: conceptualization, methodology, validation, investigation, data curation, visualization, writing—original draft, writing—review and editing, supervision, project administration, funding acquisition. F. Chaguaceda: Methodology, formal analysis, software, investigation, data curation (of FA data), visualization, writing—original draft, writing—review and editing. P. Tirozzi: Methodology, formal analysis, software, investigation, writing—review and editing. M. Tomás-Martín: Investigation, formal analysis, writing—review and editing, visualization. E. Jakobsson: Methodology, formal analysis, software, investigation, data curation (of FA data), writing—review and editing. T. Chonova: Investigation, formal analysis, writing—review and editing. B. Misteli: Validation, investigation, data curation, writing—original draft, writing—review and editing. A. Scotti and J. F. Henriques: Investigation, formal analysis, writing—review and editing. J. Rubio-Ríos, D. Morant, O. Stamenković, R. Mondav, K. Münzner, L. Bonacina, V. Nava, E. Drohan, E. Fenoy, A. Llorente, M. Mathieu-Resuge, D. Halabowski, J. Martelo, and D. Cunillera-Montcusí: Investigation, writing—review and editing. P. Marle: Visualization, investigation, writing—review and editing. V. Kolar: Formal analysis, writing—review and editing. S. Esosa. Osakpolor, N. P. D. Juvigny-Khenafou, and L. N. Nash: Investigation, writing—original draft, writing—review and editing. J. C. Fahy: Investigation, data curation, writing—review and editing. A. Balibrea: Investigation, review and editing. B. Rimcheska: Conceptualization, validation, data curation, writing—review and editing, visualization, supervision, project administration, funding acquisition.

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Conflict of Interest

None declared.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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