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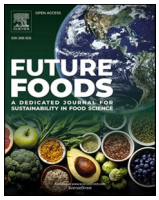

Black soldier fly larvae (*Hermetia illucens*) reared on conventional and emerging agri-food by-products: the case of olive leaves, olive pomace, and quinoa husk

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A B S T R A C T

Black soldier fly larvae (BSFL) is one of the most popular edible insects authorized for feed and an excellent bioconversor of agri-food by-products. Thus, the ability of BSFL to valorize by-products from olive oil production (olive leaves, OL, or full-fat dry olive pomace, OP) and quinoa husk (QH) is explored.

OL up to 15 %, and OP or QH up to 50 %, allowed successful bioconversion of by-products, with larvae performance comparable to control. These levels did not affect protein, lipid or ash content, though chitin increased. Mainly OP feeding resulted in more unsaturated lipids of BSFL, with lauric acid decreasing from 43 % in control larvae to 23 % in OP50 and 2.5 % in OP90, while oleic acid rose as the major one to 32 % and 55 %, respectively. However, higher inclusion of OL (>15 %) and OP (>50 %) reduced protein and ash contents, increasing lipids and chitin. QH-fed larvae showed similar composition to control. Correlation analysis suggested that unbalanced diets at high levels of OL and OP influenced the results. Diets rich in carbohydrates and proteins also correlated with the saturated profile of BSFL, while high lipids and fiber led to more unsaturated ones, particularly with OP.

Therefore, BSFL can successfully valorise olive-oil and quinoa by-products when used at limited levels, maintaining similar nutritive composition of the larvae but improving their fatty acid profile.

1. Introduction

The new regulated insect industry is under full expansion and development. Insect market is expected to reach 9.6 billion dollars (>3 million tons) at annual growth rate of 31 % during 2022–2030 (Global Edible Insects Market Report 2022–2030). In Europe, according to IPIFF (International Platform of Insects for Food and Feed), an expectation up to 260,000 tons in 2030 has been estimated (IPIFF, 2020). Specifically, since 2021, up to 4 species are already approved for food and 8 species for feed in Europe. Within them, some of the most popular are the larvae of *Hermetia illucens* (black soldier fly larvae, BSFL). Their protein contents are around 50–60 % together with around 25–30 % lipids (Hawkey et al., 2021). Proteins include all essential amino acids, and lipids are quite variable on composition depending on diets, but BSFL mainly contains saturated fatty acids as lauric acid, with special interest for food, pharmacy and cosmetics, mainly as antimicrobial lipid (Hurtado-Ribeira et al., 2023a). Fiber as chitin, and micronutrients, complete their main composition.

Concerning the insect feeding, this industry should be competitive with traditional protein sources but keeping at the same time its principle of sustainability. In this sense, the implementation of insect rearing using agri-food by-products, which is authorized for insects feeding, is

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one of the most current used strategies, achieving a revalorization of agri-food by-products into valuable products (Gasco et al., 2020; Mannaa et al., 2024; Varelas, 2019). Concerning agri-food by-products, a huge number of sources remains unexplored for insect feeding. According to IPIFF, up to a third of the food waste generated (20 million tons) could be suitable for insect farming. One example of unexplored by-products on insects are olive leaves. There are around 9 million ha of olive trees worldwide, and their leaves are one of the largest contributors to waste due to tree-pruning and harvesting. It is estimated that >1 million tons of olive leaf waste are generated just in Spain, around 50 % of the total world production (Espeso et al., 2021; Malekjani and Jafari, 2023). This waste is traditionally thrown away or burned, and its use in animal feeding is minor. Together with leaves, one of the even more problematic olive wastes is the olive mill waste, including "alperujo" or olive pomace (Foti et al., 2022; Madureira et al., 2022). For one ton of processed olives, 0.5–0.6 tons of olive pomace are produced, but its high moisture content (>60 %) causes the greatest problem for its revalorization (Madureira et al., 2022). In general, previous data on the use of olive oil or quinoa by-products in BSFL is almost negligible. Available scientific information on the use of olive oil by-products in BSFL feeding is minor. Only some few studies have described the inclusion of olive pomace, that reported reduced larval growth and bioconversion efficiency, but depending on the level of inclusion and the form of the specific type of pomace (Ameixa et al., 2023; Ramzy et al., 2022; Starcevic et al., 2019). Therefore, considering the diversity of olive pomace types generated by the olive oil industry, differing in moisture and fat content, offers a wide range of options for being explored in BSFL feeding.

Besides these conventional and well-known agri-food by-products from olive oil production, other emerging by-products from other emerging crops may be also considered as potential feeding sources for insects. As example, the world production of quinoa has almost tripled from 53,000 tons in 2000 to 149,000 tons in 2020, being established in Europe. Expanding at a rate of 11 %, the global quinoa market is projected to increase up to 1.4 billion by 2032 (Quinoa Market Outlook 2022–2032). Together with its high nutritional value in proteins, it can be grown in harsh conditions and needs less fertilizers. Therefore, FAO recommended to expand this promising and sustainable crop (Filik, 2020). However, its expansion and intensification entail a large volume of husk (around 10 % of total product), an emerging waste of poor value produced during the scarification of the grain to reduce its bitterness, due to saponins accumulated in husk (Ariaeenejad et al., 2022; Cantero-Bahillo et al., 2024). Some scarce studies have explored the use of husk for animal feeding, but with limited potential or unclear results (Carlson et al., 2012). However, previous studies on the use of quinoa husk in BSFL have not been found.

Therefore, the main aim of this study was to explore the feeding of BSFL with either conventional agri-food by-products from olive oil production, as olive leaves or olive pomace, as well an emerging by-product, as quinoa husk. Thus, the impact of these experimental diets included at different level in the diets of the larvae on productive parameters, bioconversion and nutritional composition of the larvae was tested.

2. Materials and methods

2.1. Raw materials for BSFL feeding

Dry pruning olive leaves ("manzanilla" variety) were kindly provided by Natac Biotech SL (Alcorcón, Madrid, Spain) and they were grounded to powder. Full-fat dry olive pomace as powder was kindly provided by Troil Vegas Altas SC (Vadetorres, Badajoz, Spain). Quinoa husk as powder was kindly provided by Naturquinoa (Madrid, Spain). All samples were stored sealed, at room temperature and in the dark.

2.2. BSFL rearing and processing

BSFL were reared by Entomo AgroIndustrial (Murcia, Spain). BSFL diets were based on wheat bran or partial replacement with the different by-products: dry olive leaves at 15 %, 30 % or 50 % (OL15, OL30, OL50); full-fat dry olive pomace at 30 %, 50 %, 70 %, 90 % (OP30, OP50, OP70, OP90), or quinoa husk at 15 %, 30 % or 50 % (Q15, Q30, Q50). These values were selected according to a preliminary low-scale study performed with the same diets at 50 % replacement, that allowed to observe potential mortality or apparent detrimental in the larva growth (data not shown).

Each diet (5 kg) was mixed with water to produce 15 kg of wet substrate. Substrates were distributed in triplicate in plastic trays (58 × 38 cm, inner side, with substrate dispersed to achieve a depth of 4 cm). A total number of 13,000 newly hatched larvae (91 g) were reared for each replicate of substrate for 12 days. The experiment was carried out in a climate control chamber at 26 ± 1 °C and a relative humidity of 65 ± 5 %.

After the feeding trial, larvae were sieved and washed in cool water. They were slaughtered by blanching in water at 90 °C at a ratio of sample to water of 1:10 (w/v) for 40 s according to Hurtado-Ribeira et al. (2023b). Thereafter, larvae were immersed in cold water and drained. Finally, the larvae were dried by oven drying at 55 °C for 72 h.

Remaining substrate after each replicate of feeding was also weighted and dried at 102 °C to estimate the total amount of remaining material at dry matter basis.

2.2. Productive parameters

Total larvae biomass at the end of the trial was reported and the total larvae biomass gained was estimated. Additionally, the average weight of larvae at 0, 3, 6, 10 and 12 days of feeding from each replicate of substrate was recorded taking and weighting 500 larvae from each replicate. This allowed to estimate the growth rate as average weight of larvae, as well as:

$$\text{Weight gain (WG)} = W_f - W_o \quad (1)$$

$$\text{Average daily weight gain (ADG)} = \text{WG} / \text{Total time of feeding} \quad (2)$$

where W_f is the final average larval weight, W_o is the initial average larval weight.

The feed conversion ratio (as dry to fresh matter) was estimated as:

$$\text{FCR} = (\text{Total weight of initial substrate} - - \text{Total weight of final residue}) / \text{Total weight of larvae biomass gained} \quad (3)$$

As complementary data to FCR, and according to Bosch et al. (2020), the bioconversion efficiency corrected for residue (BER) was also estimated (as fresh to dry matter), considering the residue at the end of the experiment as the mixture of remaining substrate, exuvia and excreta:

$$\text{BER} = [\text{Total weight of larvae biomass gained} / (\text{Total weight of initial substrate} - - \text{Total weight of final residue})] \times 100 \quad (4)$$

Finally, according to Bosh et al. (2020), the mass reduction and mass reduction index, as additional complementary data, both as dry matter, were estimated as:

$$\text{Mass reduction (MR)} = [(\text{Initial substrate} - - \text{Final residue}) / \text{Initial substrate}] \times 100 \quad (5)$$

$$\text{Mass reduction index (MRI)} == \text{MR} / \text{Total time of the feeding} \quad (6)$$

2.3. Proximate composition of the samples

Determination of proximate composition was carried out on both dry substrates and fresh larvae using the routine procedures of official method of analysis (AOAC, 2005) for dry matter (934.01), crude protein (954.01), lipids (920.39), and ash (942.05). The amount of crude protein was assessed by the Kjeldahl method, with a conversion factor of 6.25 for diets and of 4.43 for fresh larvae to avoid overestimation due to non-protein nitrogen compounds such as chitin, small peptides, urea, and other compounds (Smets et al., 2021). The percentage of nitrogen-free extract was estimated as the difference between the sum of crude protein, lipid and ash values and the total of macronutrients. Crude fiber was evaluated according to the Weende method. The analysis of the chitin content was performed using the method described by Finke (2007), with modifications by Marono et al. (2015). This procedure is based on the determination of acid detergent fiber (ADF) according to AOAC method 973.18, the quantification of nitrogen in the ADF fraction using the Kjeldahl method (AOAC 955.04), and the subsequent calculation of chitin content (%) as ADF (%) – ADIP (%), where ADIP refers to the amount of protein bound to the ADF fraction.

2.4. Fatty acids profile of the samples

The fatty acid profile of diets and larvae was determined. Fatty acids were transformed into their corresponding fatty acid methyl esters (FAMEs). The methylation of fatty acids was carried out according to the AOAC Official Method 996.01 (Section E), using NaOH-methanol solution (0.5 N) and BF_3-methanol solution (~14 %, w/v) as catalysts. The FAMEs were analyzed by GC according to the method described by Vázquez et al. (2017). Identification and quantification of FAMEs was carried out in an Agilent 6850 Network GC System (Avondale, US), coupled to FID detector and Agilent 6850 autosampler. The capillary column was a HP-88 (30 m, 0.25 mm i.d.) (Avondale, US). An injection volume of 1 μL and a 20:1 split ratio were used. The injector and detector temperatures were 220 and 250 °C, respectively. The temperature program started at 50 °C, rising to 220 °C at 15 °C min^{-1}. The final temperature (220 °C) was held for 10 min. Identification of FAMEs was based on the retention times and the relative area percentages of No.3 PUFA reference standard (47,085-U), obtained from Supelco (Bellefonte, US).

2.5. Statistical analysis

The statistical analysis was performed by a one-way analysis of variance using the general linear model procedure of the SPSS 26.0 statistical package (SPSS Inc., Chicago, IL, USA). Before conducting the ANOVA, the assumptions of normality and homogeneity of variances were evaluated. Normality was assessed using the Shapiro-Wilk test, and homogeneity of variances was examined with Levene's test. When the effect of any of the factors was significant ($p \leq 0.05$), differences between groups were analyzed by using the post-hoc Tukey. Pearson correlation tests were conducted for additional analyses.

3. Results and discussion

3.1. Proximate composition of the BSFL substrates

All the experimental diets (Table 1) presented a lower protein content with respect to the control diet. Moreover, these values decreased as the inclusion percentage of the by-product increased. This result was reasonable, since the starting materials (OL, OP and QH) had a lower protein content than the control diet, especially in case of OL (18 % vs 8 %, respectively). There were no differences in the lipid content of the OL and QH diets with respect to the control, in agreement with the lipid content of these by-products, which was the same as the wheat barn of the control (close to 3 %). However, the OP-based substrates showed a clear progressive increase in the lipid content with the increasing inclusion levels (from 3 % for control up to 11 % for OP90). This result was expected, since the OP had the highest lipid value (around 12 %). Concerning fiber, OL and OP showed relevant fiber contents (14 % and 19 %, respectively), compared to the wheat barn (2 %). Due to this, the fiber content increased in the diets with OL and OP as the inclusion increased; a result that did not occur with the QH diets. It should be noted that fiber content was assessed as crude fiber, which provides a general approximation but may underestimate total structural carbohydrates and fiber utilization, compared to ADF and neutral detergent fiber (NDF) fractions, which are more informative in terms of digestibility and feed intake behavior. The ash content of the experimental diets was also lower for all diets with respect to the control, as was the case with protein. This was also in agreement with the lower ash content of the tested by-products compared to the wheat barn, especially in the case of OL. In terms of estimated carbohydrates, this tended to be higher with the OL and QH inclusion, and lower with the OP inclusion. Finally,

Table 1
Nutritional composition of black soldier fly substrates (%, dry matter).

	Protein	Lipid	Fiber	Ash	NFEM [1]	GE[2]	Moisture[3]
By-products for substrates							
Olive leaves	8.42 ± 0.03*	2.83 ± 0.18	14.34 ± 0.52*	6.14 ± 0.15*	68.28	1449	7.25 ± 0.14*
Olive pomace	12.09 ± 0.38*	11.93 ± 0.26*	19.51 ± 0.25*	9.38 ± 0.43*	47.08	1536	9.29 ± 0.29*
Quinoa husk	11.73 ± 0.05*	3.68 ± 0.10	5.15 ± 0.67*	12.76 ± 0.31*	66.68	1534	10.45 ± 0.10*
Substrates formulated with by-products							
Control	18.18 ± 0.44^{a}	2.77 ± 0.03^{fgh}	2.51 ± 0.09^{h}	22.03 ± 0.10^{a}	54.51	1447	11.07 ± 0.10^{a}
OL15	16.84 ± 0.26^{b}	2.65 ± 0.02 g	3.70 ± 0.18 g	19.29 ± 0.08^{bc}	57.52	1461	9.57 ± 0.22^{cd}
OL30	15.14 ± 0.24^{cd}	2.62 ± 0.11 g	5.22 ± 0.12^{f}	16.87 ± 0.19^{d}	60.14	1464	8.77 ± 0.17^{f}
OL50	13.51 ± 0.19^{e}	2.93 ± 0.04^{efg}	7.77 ± 0.20^{d}	14.29 ± 0.16 g	61.49	1460	8.12 ± 0.09 g
OP30	16.63 ± 0.02^{b}	5.91 ± 0.14^{d}	7.15 ± 0.30^{e}	19.92 ± 0.16^{b}	50.39	1464	9.52 ± 0.00^{cde}
OP50	14.94 ± 0.27^{cd}	7.27 ± 0.13^{c}	11.50 ± 0.12^{c}	15.25 ± 0.32^{f}	51.04	1488	9.27 ± 0.36^{de}
OP70	14.35 ± 0.21^{de}	9.50 ± 0.11^{b}	14.99 ± 0.28^{b}	13.50 ± 0.31^{h}	47.65	1504	9.10 ± 0.17^{def}
OP90	12.62 ± 0.42^{f}	10.82 ± 0.13^{a}	19.98 ± 0.23^{a}	10.48 ± 0.38^{i}	46.10	1488	9.04 ± 0.12^{ef}
QH15	16.37 ± 0.19^{b}	2.72 ± 0.08^{fgh}	2.35 ± 0.03^{h}	19.60 ± 0.11^{bc}	58.95	1477	10.06 ± 0.14^{b}
QH130	15.46 ± 0.39^{c}	2.97 ± 0.10^{ef}	2.59 ± 0.19^{h}	19.05 ± 0.25^{c}	59.93	1481	9.83 ± 0.09^{bc}
QH50	14.96 ± 0.33^{cd}	3.14 ± 0.04^{e}	3.20 ± 0.15 g	16.08 ± 0.07^{e}	62.63	1521	9.56 ± 0.09^{cd}

[1] NFEM (nitrogen free extractive matter).
[2] G.E. (gross energy) calculated using the energy coefficients of Miglavs & Jobling (1989): protein 23.6 kJ/g, lipids 38.9 kJ/g and carbohydrates 16.7 kJ/g and expressed as kJ/100 g of dry matter.
[3] Value for fresh diets (g/100 g) before hydration with 1:2 water. OL, dry olive leaves; OP, full-fat dry olive pomace; QH, quinoa husk. Different letters in the same column within the substrates formulated with by-products results (a-i) indicate significant differences ($p \leq 0.05$).
* in the same column within the by-products for substrates indicate significant difference respect to the control ($p \leq 0.05$).

the gross energy of the substrates was estimated, and values between 1450–1534 kJ/100 g were obtained.

It should be noted that the by-products used exhibited lower inherent moisture content compared to the control diet (Table 1). As a result, increasing inclusion levels of these ingredients led to slightly drier dry diets. Nevertheless, since the moisture content was quite similar (9–11 %) and considering that all these dry diets were uniformly mixed with 67 % of water to produce the final given substrate, the relative differences in initial moisture content could be considerably diluted.

3.2. Productive parameters of BSFL

Most of the experimental diets evaluated in this study allowed the development and growth of BSFL larvae, although with significant differences depending on the substrates. Fig. 1 presents the results obtained on the impact of the diets on larval growth. The control larvae reached a final average weight of 163.7 ± 15.7 mg per larvae after 12 days of growth. This result was comparable with other studies, since the typical final weight of BSFL, and previous to pre-pupae, used to be in the range of 150–190 mg (Ameixa et al. 2023; Belperio et al., 2024; Rossi et al., 2023; Scieuzo et al., 2023).

The diets prepared with OL at the highest levels of inclusion (30 % and 50 %) (Fig. 1.A) caused a notable slower growth rate of the larvae compared to the control diet, whereas OL15 maintained a similar growth rate to wheat barn. Thus, OL30 and OL50 diets caused a 50 % and 70 % reduction of the growth, reaching final weights of 84.6 ± 1.7 mg and 50.2 ± 6.6 mg, respectively.

In the case of OP (Fig. 1.B), the 30 % and 50 % inclusion levels caused slightly higher growth rate than the control group until day 6 of feeding. However, from that moment on, the growth rate slowed down respect to the control. This caused that the final growth was 23 % lower for OP30 and OP50 with respect to the control (126.2 ± 15.2 and 126.1 ± 9.4 mg respectively). OP70 also maintained a similar behaviour to the control until day 6; but after that, it slowed down more remarkably than OP30 and OP50. Thus, OP70 decreased the final growth by 40 % respect to the control (98.7 ± 19.2 mg). Finally, the OP90 treatment caused the slowest growth rate, these larvae reaching only the 36 % of the control weight at the end of the feeding assay (58.3 ± 8.8 mg).

The diets prepared with QH (Fig. 1.C) stood out for their performance, since, in general, up to day 6, all inclusion levels showed a relevant higher growth than the control. Especially, it was remarkable that QH30 caused an extremely fast growth in the first 3 days, these larvae reaching approximately 117 % higher weight than the control group at day 3 of feeding (127.5 ± 20.9 mg and 58.5 ± 2.5 mg, respectively). However, after that moment, this rate stabilized, reaching a final similar weight to that of the control. In fact, the final weight seemed to decrease for QH30 at day 12 of feeding but this was due to some pre-pupae that started to emerge. QH15 and QH50 treatments, being very similar to each other, also showed growth rates higher than that of the control (approximately 20 %) until day 6. After this point, the growth rate was lower. Therefore, these larvae showed a final 13 % reduction of the weight for QH15 (141.7 ± 31.7 mg) and 27 % for QH50 (118.7 ± 14.6 mg).

The final estimated values of WG and ADG after the 12 days feeding are detailed in Fig. 2. These results agreed with the general differences and patterns due to the experimental substrates described for the growth rates (Fig. 1). Thus, the larvae of the control group (Fig. 2) obtained the highest WG and ADG (156.7 ± 15.7 mg/larva; 13.7 ± 1.3 mg/day). These values were comparable to the WG and ADG of the larvae from the OL15, QH15 and QH30 treatments. On the contrary, the rest of the diets caused a significant lower WG and ADG than the control group, which evidences the impact of the applied treatments on the development and growth of BSFL larvae. Thus, in general, a significant decrease in larval WG and ADG was observed as the percentage of any of both olive by-products inclusion increased. In the QH-treated group, a significant decrease in the final growth was only detected with the Q50 diet.

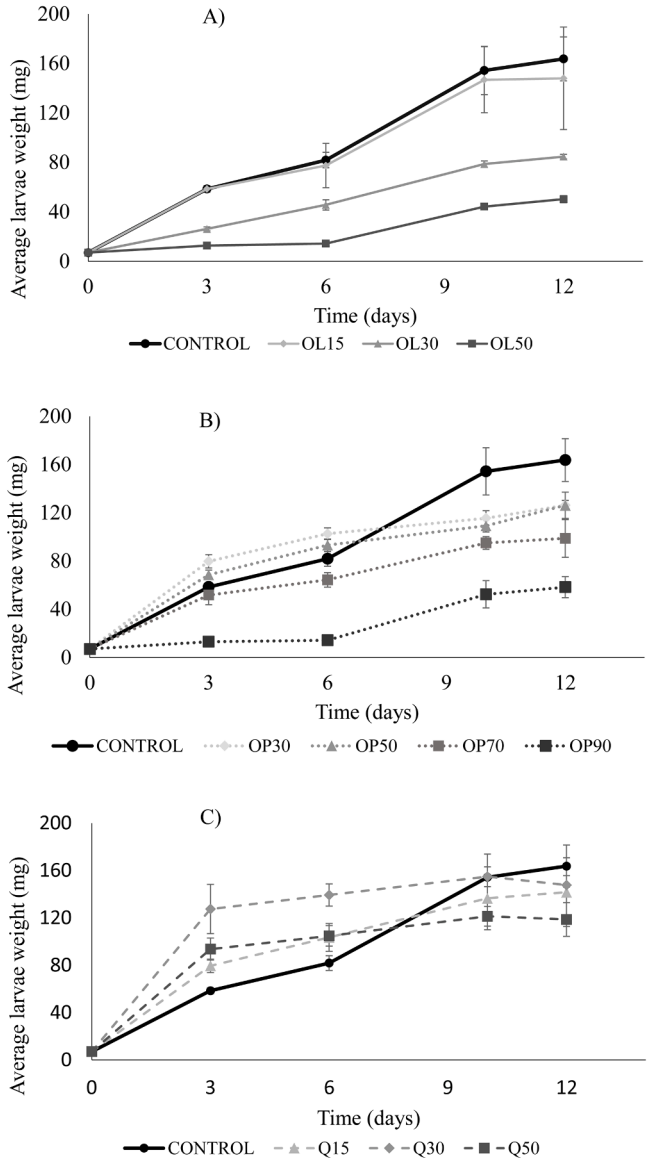

Fig. 1. Average larvae weight (mg) of BSFL during the feeding with the control substrate vs OL (dry olive leaves, A); OP (full-fat dry olive pomace, B) and QH (quinoa husk, C) substrates at different levels of inclusion.

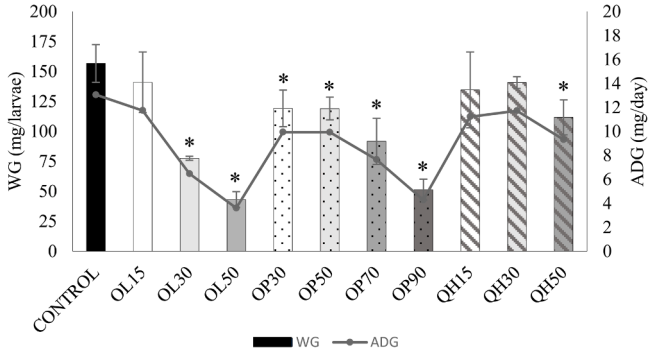

Fig. 2. Weight gain (WG) and average daily gain (ADG) of BSFL after the feeding with the control substrate vs OL (dry olive leaves), OP (full-fat dry olive pomace), QH (quinoa husk). * shows significant differences with respect to the control.

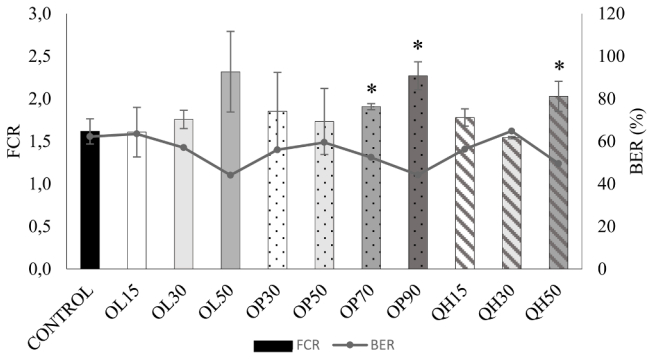

Fig. 3. Feed Conversion Ratio (FCR) and Bioconversion efficiency (BER) of BSFL after the feeding with the control substrate vs OL (dry olive leaves), OP (full-fat dry olive pomace), QH (quinoa husk). * shows significant differences with respect to the control.

The estimated FCR and BER of the larvae is shown in Fig. 3. The control group exhibited a FCR of 1.6 ± 0.1 (Fig. 3), a value comparable to most treatments at the lowest values, except for the highest values of OP70, OP90, and QH50, which showed significant higher values than the control (1.91 ± 0.03, 2.3 ± 0.2, and 2.0 ± 0.2, respectively) and the same trend was observed for OL50. This indicated a clear impact on FCR with increasing inclusion levels of OP in the diets of BSFL, as well as the highest level of QH and OL. Conversely, the BSFL showed a BER of 62.2 ± 5.7 % (Fig. 3) and the same significant differences due to the treatments for FCR were obtained. Thus, OP70, OP90 and QH50, caused significant lower values of BER of 52.4 ± 1.0 %, 44.2 ± 3.2 % and 49.6 ± 4.4 %, respectively, and a same trend was observed for OL50.

Due to the major interest of this study about the potential bioconversion and reduction of by-products by BSFL, the MR and MRI were estimated and shown in Fig. 4. Larvae in the control group showed a MR of 65.4 ± 6.8 % at rate of 5.5 %/day, with no significant differences compared to larvae in the OL15, OP30, OP50, QH15, and QH50 groups. However, the rest of the treatments (OL30, OL50, OP70, OP90) caused significant lower MR values compared to the control, indicating that as the percentage of both olive by-product inclusion increased, the MR values worsened. A remarkable result was that only in case of QH30, a significant higher MR was obtained (77.6 ± 0.9 % at rate of 6.5 %/day) respect to the control. This would suggest that this treatment caused the most efficient reduction of substrate by the larvae. This was an interesting result, since QH30 larvae reached the same final productive parameters than the control larvae (WG, ADG, FCR and BER), but with the additional advantage of causing an improvement on the reduction of the substrate, and hence, on the quinoa husk by-product. This better MR value agreed with the extremely fast growth rate previously observed for

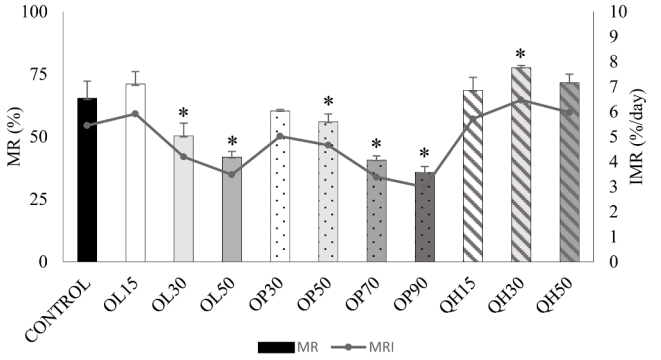

Fig. 4. Mass reduction (MR) and mass reduction index (MRI) of BSFL after the feeding with the control substrate vs OL (dry olive leaves), OP (full-fat dry olive pomace), QH (quinoa husk). * Shows significant differences with respect to the control.

this treatment (Fig. 1).

It should be noted that, although larval mortality of the treated larvae was not performed in this study, no visible mortality was observed during the trials. In treatments where growth performance was reduced, larvae just appeared smaller in size, suggesting that larval densities remained relatively consistent throughout the experimental period. Nevertheless, future studies should include precise survival measurements to strengthen the robustness of bioconversion and performance results.

Most of the differences observed in larval growth and productive parameters of BSFL due to the diets used in this study are likely attributable to the nutritional composition of the experimental substrates. Therefore, a correlation analysis between production parameters and each nutrient (Table 1) was conducted, revealing notable relationships. First, an initially global correlation analysis was performed considering all the diets, in order to evaluate the impact of the proportion of each nutrient for all the 11 substrates, regardless of the specific experimental by-product. Thus, in general, the higher the protein content of the substrates, the better productive parameters ($p < 0.05$). This same positive effect was observed for the ash content ($p < 0.05$). On the contrary, the higher the fiber content, the lower the WG ($r=-0.647$, $p = 0.032$) and MR ($r=-0.839$, $p = 0.001$). As consequence, the higher the protein to fiber ratio of the diets, the better productive parameters ($p < 0.05$). This positive effect on production was also observed for the higher lipid to fiber ratio ($p < 0.05$). Therefore, all these results suggested that these nutritional components of the substrates are determinant for the efficient growth of BSFL, especially a high protein and ash content, together with a low fiber content, regardless of other minor compounds or attributes that the different experimental by-products conferred to the substrates.

In the specific diets formulated with OL, it was confirmed a strong linear correlation for protein ($r = 0.985$, $p = 0014$) and ash ($r = 0.972$, $p = 0.028$) content of the diets, but in this case, only for the WG parameter. Furthermore, the strong and linear negative impact of fiber of OL diets was also demonstrated, for both WG ($r=-0.972$, $p = 0.028$) and BER ($r=-0.951$, $p = 0.049$). In case of OL, it is interesting to remark that the carbohydrates content of the diets, also negatively impacted on WG ($r=-0.956$, $p = 0.044$). As consequence, the higher the ratio protein to carbohydrate, the better WG ($r=-0.975$, $p = 0.025$). Therefore, these results would suggest that the worst observed growth for BSFL as the level of OL increase, may be strongly related to the unbalanced content of low protein, high carbohydrates and high content of fiber of the substrates.

In diets formulated with OP, it was also demonstrated the strong linear correlation for protein ($r = 0.955$, $p = 0012$) and ash ($r = 0.929$, $p = 0.023$) contents of the diets on WG. These nutrients were also significantly related to the MR ($p < 0.05$). This would suggest that the lower growth for OP-based diets may be related to lower consumption of substrate due to the nutritional compositions of the substrates. Furthermore, in case of OP, the carbohydrates content of the diets positively impacted on all productive parameters ($p < 0.05$), and the lipid content negatively affected ($p < 0.05$). As consequence, the higher the ratio lipids to carbohydrates of OP diets the worse the productive parameters ($p < 0.05$). Furthermore, the strong and linear negative impact of fiber of OP diets was also demonstrated, for both WG, BER and MR ($p < 0.05$). Therefore, it can be concluded that the unbalanced high lipid and low carbohydrate contents of the diets caused by the inclusion of OP, together with the higher fiber content, may be the main reasons of the lower growth of the larvae fed on OP-based diets.

Finally, in the case of quinoa husk, probably due to the similarity in most nutrients respect to wheat bran of control (Table 1), no significant correlations were found between most productive parameter and macronutrients of the substrates. This points out quinoa husk as an interesting alternative and sustainable substrate for BSFL with a great potential, due to the current lack of commercial value of this by-product.

Considering the contribution of the macronutrients and

micronutrients in diets is crucial to ensure optimal larval growth and development, as observed in previous studies with other agri-food by-products tested for BSFL. In general, previous data on the use of olive oil or quinoa by-products in BSFL is almost negligible. Only few examples were found for olive pomace. Our results are in agreement with those reported by Ameixa et al. (2023), who evaluated BSFL growth using different percentages (25 %, 50 % and 75 %) of olive pomace inclusion. However, in such study it is not clearly said what type of olive pomace was used, wet or dry, or full-fat or defatted pomace. It could be understood that it was partially defatted pomace, according to the lipid content given for the substrates (estimated as 5 % for olive pomace vs >10 % in the present study for the used full-fat dry olive pomace). Nevertheless, in such study, it was similarly observed that as the percentage of olive pomace in the diet increased, the growth of BSFL larvae was lower compared to the control group. Also, both reduction of substrate and bioconversion progressively decreased with increasing inclusion percentage, which is consistent with the results obtained in the present study. Other examples can be found for olive pomace in BSFL, but it was used as defatted olive pomace (Ramzy et al., 2022) or it was used at 100 % levels (Starcevic et al., 2019). Concerning other agri-food by-products, in the study by Taufek et al. (2024), the growth of BSFL larvae fed with 5 diets based on agri-food by-products was evaluated. The observed differences between the diets on growth performance were related to the higher protein and lipid content in the animal by-products. This trend was also observed in another study by Belperio et al. (2024), where the effect of four diets on the growth of BSFL larvae was evaluated: a control diet, a vegetable diet, an omnivorous diet and a carnivorous diet. Overall, the diet with the best results was the control diet. Furthermore, no significant differences were found with the omnivorous and carnivorous diet, unlike the vegetable diet, which showed the worst results, related to the lower content in macronutrients, essentially protein, carbohydrates and lipids. This evidence reinforces the importance of nutritional content in the development of BSFL. In fact, the protein and carbohydrate dietary contents, but specially the protein/carbohydrate ratio are being evidenced as important parameters in larval development. Concerning the protein requirements of BSFL, Bellezza Oddon et al. (2022a) established a value of 16 % as the optimal protein level, considering the whole larval stage. Therefore, in agreement, several experimental substrates of this study failed to be close to this requirement at the highest inclusion levels in the diets, mainly in case of olive oil by-products (OL50, OP70, OP90; Table 1). Furthermore, there are diverse studies that have explored the relevance of the ratio protein/carbohydrate (Barragan-Fonseca et al., 2019). As recent example, Eggink et al. (2023) evaluated the impact of BSFL growth with different protein/carbohydrate ratios and concluded that the optimal ratio was in the range of 1:2–1:3, close to the findings of other previous studies. This value agrees with that of the diet used for the control larvae of the present study (1:3), as well as with most of treatments of OP and QH (in the range of 1:3–1:3.9). However, in case of OL, it was clearly demonstrated a strong linear relationship between the WG and the protein to carbohydrate ratio, as previously commented. Thus, the poorest WG observed for OL50 corresponded to the highest ratio of 1:4.6 estimated for this diet, whereas the best WG corresponded to the control at 1:3. This reinforces the idea of maintaining an adequate balance of these macronutrients in the range of 1:2–1:3, to maximise larval growth, and that such obtained unbalanced ratio that increased with olive leave inclusion, together with the high fiber content, may be the most important factors that explained the observed growth results for olive-leave based diets.

On the other hand, Naser El Deen et al. (2023) also demonstrated in their study the influence of fat content on BSFL growth. In terms of productive parameters, the diet based on fast food waste, which had a higher fat content, showed the best results compared to the control group and the rest of the diets. However, this was not in agreement with the current study, since in the case of OP, the high lipid content of these diets was related to the poor growth performance in larvae fed the highest inclusion percentages of OP. The studies about the impact of dietary lipids on BSFL and the specific requirements are still scarce. Belleza Oddon et al. (2022b) concluded that lipid contents $\leq$ 1 % of in the substrates have a negative effect on growth. However, the maximum admitted level of lipids in BSFL substrates has not been stablished and studies about this factor are still needed. In this sense, Li et al. (2022) evidenced that the impact of this macronutrient is related to the specific fatty acid profile of the lipid source. Thus, these authors found that growth and size of BSFL fed with linseed oil, peanut oil, coconut oil and fish oil significantly increased when these dietary lipids increased from 5 % to 10 % in the diets. However, the growth remained unchanged when soybean oil and lard oil were used. Interestingly, these authors identified the fatty acid C16:0 (palmitic acid) as being positively related to the final weight of the larvae.

Together with the impact of macronutrients, the potential positive or negative impact of specific minor molecules of the experimental by-products on growth parameters of BSFL should be also considered. Thus, some minor dietary molecules have been suggested to be potential antinutrients for feeds, as the case of tannins or polyphenols (Ameixa et al., 2023). This relationship was effectively demonstrated also in the present study. Thus, when we stablished a correlation study between the total phenolic content of the diets (data not shown) and the growth parameters, significant values were found for FCR (r = 0.720, p = 0.012), MR (r=−0.886, $p < 0.001$) and it was especially strong for WG (r=−0.923, $p < 0.001$). This relationship is illustrated in Fig. 1S as supplementary material. This was considered an interesting result, since despite the suggested antinutritional effect of phenolic compounds in the scientific literature, scarce studies have clearly evidenced such relationship when feeding increasing levels of phenolic compounds to BSFL. Therefore, these results suggested that these minor components of the substrates can be also determinant for the efficient growth of BSFL, regardless of the nutritive composition that the different experimental by-products conferred to the substrates. Nevertheless, it should be considered that the total phenolic content of the diets was measured using the Folin-Ciocalteu method, which is not entirely specific to phenolics and may be affected by other compounds. Therefore, for more accurate quantification, and exhaustive study of the found evidence of dietary phenolics on larvae growth more specific analytical tools are necessary.

As summary, the results of the present study confirm the great versatility of BSFL to convert agri-food by-products, and reinforce the importance of key macronutrients, such as proteins, lipids and carbohydrates, and their proper balance, in larval growth and development, as well as the potential antinutritional effect of dietary minor compounds as phenolics. Furthermore, it should be also remarked that all treatments were stopped at the same fixed time of 12 days for comparative purposes. However, those larvae with lower growth at this moment, may still need additional days to reach prepupa stage, at it has been observed in diverse studies when by-products and wastes, in general unbalanced diets, are used (Guil-Guerrero et al., 2020; Renna et al., 2024).

3.3. Proximate composition of BSFL

The nutritional composition of the BSFL fed the different experimental diets is shown in Table 2. Furthermore, the moisture content of the fresh larvae after feeding is also included. Concerning this major component of the fresh larvae, some slight significant differences were observed after the feeding. Thus, for OL-based substrates, a progressive increase in the moisture content of the larvae was obtained with the level of inclusion of OL. For the rest of diets, despite slight differences on moisture content, these did not differ from the control larvae.

Protein was the major macronutrient of the larvae, in the range of 23–32 %. The control larvae showed values according to the expected for BSFL, close to 30 % (Fabrikov et al., 2021; Melenchón et al., 2021; Rodríguez-Rodríguez et al., 2024). Concerning the impact of the diets,

Table 2
Proximate composition (g/100 g of dry matter) of the black soldier fly larvae fed the different experimental substrates.

Substrate	Protein	Lipids	Chitin	Ashes	Moisture*
Control	31.9 ± 0.4 ^{a}	11.5 ± 5.2 ^{b}	3.9 ± 0.7 ^{d}	23.6 ± 0.7 ^{abc}	71.5 ± 1.1 ^{bcde}
OL15	31.4 ± 1.3 ^{a}	8.2 ± 1.5 ^{b}	9.3 ± 1.7 ^{bc}	26.3 ± 0.8 ^{a}	72.1 ± 1.0 ^{bc}
OL30	24.4 ± 0.9 ^{de}	21.2 ± 3.0 ^{a}	9.7 ± 1.2 ^{bc}	20.2 ± 1.1 ^{bcd}	73.1 ± 0.4 ^{ab}
OL50	23.4 ± 0.7 ^{e}	14.9 ± 2.3 ^{ab}	11.4 ± 1.6 ^{ab}	20.9 ± 0.2 ^{bcd}	74.9 ± 0.8 ^{a}
OP30	30.3 ± 1.5 ^{ab}	10.2 ± 4.2 ^{b}	8.9 ± 0.7 ^{bc}	20.5 ± 1.1 ^{bcd}	69.4 ± 0.4 ^{e}
OP50	32.1 ± 1.0 ^{a}	11.0 ± 2.4 ^{b}	9.3 ± 0.3 ^{bc}	19.6 ± 0.7 ^{cd}	69.6 ± 0.8 ^{de}
OP70	27.4 ± 0.7 ^{bcd}	16.3 ± 1.9 ^{ab}	15.3 ± 1.4 ^{a}	16.8 ± 0.4 ^{d}	69.6 ± 0.6 ^{de}
OP90	26.5 ± 2.5 ^{cde}	20.9 ± 3.1 ^{a}	11.0 ± 3.3 ^{bc}	17.0 ± 0.9 ^{d}	69.8 ± 0.6 ^{cde}
QH15	30.8 ± 1.3 ^{ab}	8.2 ± 2.1 ^{b}	6.9 ± 0.5 ^{cd}	24.4 ± 1.3 ^{ab}	71.9 ± 1.3 ^{bcd}
QH30	30.0 ± 0.8 ^{abc}	8.7 ± 2.8 ^{b}	7.2 ± 1.0 ^{cd}	24.2 ± 1.7 ^{ab}	72.1 ± 0.9 ^{bc}
QH50	29.8 ± 1.4 ^{abc}	12.7 ± 3.5 ^{ab}	8.5 ± 0.5 ^{bc}	20.9 ± 4.0 ^{bcd}	72.2 ± 0.5 ^{b}

* Value for fresh larvae (g/100 g of fresh larvae). Different letters within the same column mean significant differences ($p \leq 0.05$).

most of the experimental substrates based on olive oil by-products caused a trend to lower protein content in the larvae, but being evident at the highest levels of inclusion tested. Thus, in case of OL, values higher than 15 % of inclusion dramatically decreased the protein content (from 32 % for control diet up to 23 % for OL50). In fact, correlation studies between the diet and larvae compositions showed that, although no significant ($p > 0.05$), the protein content of the larvae tended to increase with the protein and ash contents of the diets, and to decrease with the fiber content of the diets. Furthermore, it was also significantly evidenced that the lower the WG and MR during the feeding with levels of OL, the lower the protein content of the larvae ($r = 0.982$, $p = 0.018$; $r = 0.962$, $p = 0.038$, respectively).

In case of OP, values higher than 50 % of inclusion also decreased the protein content (from 32 % for control diet up to 27 % for OP90). Significantly, the lower the carbohydrate content of substrates with OP, the lower the protein content of larvae ($r = 0.909$, $p = 0.032$). This was an interesting result since the OP-based diets were remarked by a significant different nutritional composition respect to control, with lower protein, and carbohydrate contents, and relevant higher lipid contents (Table 1). But, among all these nutrients, it seems that the noticeable lower carbohydrate content of OP-based diets was the most remarkable one that conditioned the final lower protein content of the larvae fed on OP. Additionally, the protein content of the larvae fed on different levels of OP was positively correlated with the WG, BER and MR ($p \leq 0.05$). The limiting factor found for carbohydrates in case of OP may have sense, since carbohydrates are the main energy source of BSFL, but they can also act as backbones for certain amino acids (Eggink et al., 2023). Furthermore, a diet with an adequate energy from carbohydrates may prevent the use of proteins as energy source, allowing proteins to be used for growth (Eggink et al., 2023). According to Table 1, the diets with increasing levels of OP were those that more negatively impacted the level of carbohydrates of the substrates.

In case of QH-based diets, due to the similar protein content of the control and QH-based diets, lack of significant differences on the final protein content of the larvae were obtained when QH was tested (Table 2).

Concerning estimation of proteins, it should be noted that this was performed based on the Kjeldahl method, but with a conversion factor of 4.43 to avoid overestimation due to non-protein nitrogen compounds such as chitin, small peptides, urea, and other compounds (Smets et al., 2021). However, it should be considered that in case of modification of these non-protein nitrogen compounds due to the experimental diets, the conversion factor may also vary. Therefore, for a more exhaustive protein quantification it would be necessary to estimate the specific conversion factors via amino acid profiling for each specific batch of larvae. However, despite this limitation, for practical reasons we applied the same 4.43 factor uniformly across all samples, as is frequently done in these types of feeding studies.

Lipids are the second most important macronutrient on BSFL. According to Barragan-Fonseca et al. (2017), lipid content of BSFL vary substantially due to substrates (from 7 % to 39 % dry matter). In agreement, as shown in Table 2, the obtained larvae in this assay showed low to medium values, in the range of 8–21 %, depending on the diet. The control larvae showed an intermediate lipid content of 12 %. This was considered a low value, probably due to an insufficient number of days for complete larval development, because as previously commented, all treatments were stopped at the same fixed time of 12 days for comparative purposes. Concerning the impact of the diets, for OL and OP, and contrary to the observed for proteins, a trend to higher lipid content of larvae was observed with the inclusion of these olive oil by-products (Table 2). In fact, values of lipid content almost duplicated respect to control larvae (21 % for OL30 and OP90, respect to 12 % for control larvae). In case of OL, a lack or relationship was found between the lipid content of the larvae and any of the nutritional components or growth parameters ($p > 0.05$). In fact, the intermediate inclusion value, OL30, was the one that showed the highest lipid content (21 % respect to 12 % for control larvae), showing a lack of dose-response pattern. Thus, it may be thought that other different components of the diets based on OL, as minor compounds, together with the final ingested level and metabolism, may condition the lipid metabolism of the larvae that favoured lipid accumulation or lipogenesis in case of OL30. In case of OP, the lipid content of the larvae was likewise not determined by any nutritional component of the diets ($p > 0.05$), although a trend to higher lipid content of larvae with the lipid content of the OP-diets could be observed. Interestingly, it was found that the higher the lipid content of the larvae with OP in the diets, the lower WG ($r = -0.882$, $p = 0.048$), BER ($r = -0.908$, $p = 0.033$) and MR ($r = -0.924$, $p = 0.025$) values. As previously concluded, the unbalanced lipid and carbohydrate contents of the diets caused by the inclusion of OP, together with the higher fiber content, may be the main reasons of the lower consumption of substrate and growth of the larvae fed on OP-based diets. As consequence of all these unbalances, higher lipid contents were accumulated in these larvae despite the worse growth.

In case of QH, a slight trend to higher lipid content of larvae was also observed with the level of inclusion of this by-product. Nevertheless, as observed for the proteins, due to the similar lipid content of the control and QH-based diets, lack of significant differences on the final lipid content of the larvae were obtained when QH was tested (Table 2).

The chitin content of the experimental larvae was also found to be significantly modified by the substrates. The most noticeable result was that all experimental by-products caused an increase in the chitin content of the larvae, respect to the control larvae, which showed values close to 4 % of chitin (Table 2). This value of control larvae was similar to those reported by previous studies (Adamaki-Sotiraki et al., 2024; Eggink et al., 2022). However, this component reached values up to 11 % for the highest tested level of OL50, 15 % for OP70, and 8.5 % for QH50. Different reasons for these results may be considered, according to the correlation tests performed for each by-product. Thus, in case of OL, significant negative relationship was obtained for the ratio protein to fiber ($r = -0.964$, $p = 0.036$) and lipids to fiber ($r = -0.972$, $p = 0.028$).

Thus, the lower these ratios of the diets, the higher the chitin content of the larvae, suggesting a potential relationship between chitin and the fiber content of the OL-based diets. In agreement, Galassi et al. (2021), testing different by-products in BSFL feeding, also found higher chitin contents on the larvae fed on brewer's grains that the authors related to the fiber content of the substrates. According to such study, the efficiency of BSFL in utilizing fiber is lower compared to non-fibrous carbohydrates, explaining the observed slower growth and weight gain in BSFL by these authors. In case of OP, despite the chitin content of the larvae was not significantly related to any nutritional component of the diets, the higher fiber content of these diets (Table 1) may also be involved in the high chitin content of the larvae. In case of QH-based diets, the chitin content of the larvae was negatively related to the protein (r=−0.980, p = 0.020) and ashes (r=−0.950, p = 0.050) of the diets. Thus, the lower the contents of these nutrients in the substrates, the higher the content of chitin. In general, the available information about the relationship between the substrate composition and chitin content is really scarce in BSFL, and most studies have related the chitin content of BSFL to the growth rate and development time (Adamaki-Sotiraki et al., 2024). In the current study, this relationship was evidenced when considering all the 11 diets, regardless of the experimental by-product. Thus, the chitin content of the larvae was significantly higher when the WG (r=−0.690, p = 0.019) and MR (r=−0.726, p = 0.011) were lower, regardless of the type of diet. In this sense, we agree with Galassi et al. (2021) that smaller larvae, as the obtained in the present study for most experimental diets due to lower WG, can have a higher surface-to-volume ratio, likely increasing the relative amount of chitin on the exoskeleton surface in the larvae. However, beyond the relationship to the size and growth of the larvae, further studies are still needed to understand the relationship between the diet composition and the chitin content of edible insects.

Finally, concerning ashes, it should be remarked that untypical high contents were found in the larvae. These values used to be closer to 10 % for BSFL (Eggink et al., 2023; Rodríguez-Rodríguez et al., 2024) rather than the values higher than 20 % obtained in this study. However, considering that all the diets, including the control substrates, already contained untypical high ashes values, this would be the main reason of the obtained ashes contents. Despite these values, significant differences were caused by the substrates, with a trend to decrease with the inclusion levels of by-products. In general, regardless of the by-product, the ashes content was obviously significantly related to the ashes contents of the diets (r = 0.804, p = 0.003), but also positively related to the protein and carbohydrates ($p < 0.05$). On the contrary, the higher the lipids and fiber contents of the diets, the lower the ashes contents of the larvae ($p < 0.05$). As consequence, the lower the ratios protein to lipids and protein to fibers of the substrates, the lower the ashes of the larvae ($p < 0.05$). Furthermore, the lower the WG, BER and MR, the lower the ashes contents of the larvae ($p < 0.05$). It has been suggested that the ash content is proportional to the development time of the larvae and the development of the exoskeleton (Fitriana et al., 2022). This would agree with the fact that those treatments that caused lower growth may have lower development and hence, lower ash content.

As summary, considering all the results together, it can be generally concluded, with some exceptions, that the tested experimental by-products tended to produce larvae with lower protein and ashes contents, and higher lipids and chitin concentration as the level of inclusion of by-products in the diets increased. However, it should be remarked that it is possible to use olive leave up to 15 %, olive pomace up to 50 %, and quinoa husk up to 50 %, to produce larvae with the same protein content than the control diet, which is the major and most important macronutrient desirable for BSFL meals. Furthermore, for these concluded ratios of inclusion of these by-products, the lipid and ashes contents would also be the same than control diets, and only higher chitin contents would be obtained in these larvae. This should not be considered a total undesirable result. Despite some studies remark the negative digestive impact of chitin, the advanced findings are demonstrating that animals possess chitinase activity at gastrointestinal tract, especially in case of omnivores compared with carnivores and herbivores (Tabata et al., 2018). Thus, this would allow to use the beneficial bioactive properties that have been also described for chitin (Wijesekara and Xu, 2024). However, specific studies would be necessary to evaluate the impact of the specific level of chitin enrichment for these larvae meals on digestibility assays or in vivo assays.

3.4. Fatty acid profile of BSFL substrates and larvae meals

The fatty acid profile of the experimental diets and the BSFL fed such substrates is shown in Table 3. The control diet of the larvae based on wheat bran was mainly based on polyunsaturated fatty acids (PUFA, 53 %), followed by monounsaturated fatty acids (MUFA, 32 %) and saturated fatty acids (SFA, 16 %). The major fatty acids were linoleic acid (48 %), oleic acid (31 %) and palmitic acid (12 %). This fatty acid profile was, in general, quite similar when the inclusion of the experimental by-products from olive leave and quinoa was performed in the diets. However, a noticeable modification of the diet was caused by the inclusion of olive pomace. Thus, these diets tended to contain higher MUFA as the level of inclusion increased (from 32 % for control up to 67 % for OP90). As consequence, the PUFA decreased (from 53 % for control up to 17 % for OP90). This was mainly due to a relevant enrichment on oleic acid and detriment of linoleic acid. This was an expected result, due to the high lipid content of the full-fat dry olive pomace used (Table 1), representing the typical fatty acid profile of olive oil (Table 3).

The fatty acid profile of control larvae showed the expected composition for BSFL (Table 3). Thus, this fat was mainly saturated (71 %), due to lauric acid as the major fatty acid (43 %), followed by palmitic acid (14 %). As unsaturated fatty acids, oleic acid (13 %) and linoleic acid (10 %) were the most representative of control larvae. However, relevant changes on the fatty acid profile were caused by the feeding with the experimental substrates, mainly those based on olive pomace. Thus, progressive lower SFA (from 71 % up to 23 % at OP90) and higher MUFA (from 17 % up to 59 % at OP90) contents were evidenced in the larvae with the level of inclusion of olive pomace. Thus, the typical fatty acid profile of BSFL was radically changed, being a totally different fat for this animal, where the lauric acid changed from being the major representative of the fat (43 %), to be a minor fatty acid (3 %). And, contrarily, oleic acid was in this case the major fatty acid (up to 55 % for OP90) together with linoleic acid (15 %). Furthermore, an intriguing result was that the saturated palmitic acid tended to increase in the larvae with OP, despite OP-based diets were similar to control diets for this fatty acid. Therefore, all these results evidence that the fatty acid composition of substrates is reflected on the fatty acids of the larvae, but also, metabolic changes take place. These findings confirm the great plasticity of the lipids of BSFL due to the diet, as it has been already evidenced in diverse studies of BSFL feeding with variable by-products substrates (Barroso et al., 2019; Ewald et al., 202; Rodrigues et al., 2022).

Respect to the results for OL-based diets, also a slight decrease on SFA and increase of PUFA was observed in the larvae, but at the highest replacement of OL50. In case of QH-based diets, the fatty acid profile remained quite similar to control larvae.

The fatty acid profile of BSFL, and its unique major fatty acid lauric acid, has been mainly related to the particular metabolism of these animals. BSFL have a great ability for the conversion of macronutrients, mainly carbohydrates, to acetyl-CoA, by the glycolysis, acetyl-CoA carboxylase and then fatty acid synthesis pathway (Ewald et al., 2020). Thus, the higher the nutritive balance of diets on these macronutrients, the higher the accumulation of lauric acid and global SFA. This relationship on the accumulation of lauric acid was significantly found in the current study for both carbohydrates and proteins, regardless of the experimental by-product ($p < 0.05$). On the contrary, the higher the lipid and fiber content of the diets, the lower the lauric

Table 3
Fatty acid profile (g/100 g of fatty acids) of the used by-products used for the formulation of substrates, the formulated substrates, and the larvae after the feeding with such substrates.

	Substrate											Larvae											By-products		
	C	OL15	OL30	OL50	OP30	OP50	OP70	OP90	QH15	QH30	QH50	C	OL15	OL30	OL50	OP30	OP50	OP70	OP90	QH15	QH30	QH50	OL	OP	QH
C10:0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.2	0.9	0.5	0.9	0.6	0.3	0.1	1.2	1.1	1.1	0.0	0.0	0.0
C12:0	0.2	0.1	0.2	0.2	0.0	0.0	0.1	0.0	0.1	0.1	0.6	42.9	44.5	42.2	30.9	29.8	22.9	11.2	2.5	42.3	42.4	44.5	0.8	0.1	0.3
C14:0	0.1	0.3	0.4	0.6	0.0	0.0	0.1	0.0	0.2	0.2	0.6	9.5	8.8	9.2	7.5	5.7	4.4	2.5	0.8	8.7	8.9	9.2	3.3	0.1	1.1
C14:1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.5	0.4	0.5	0.3	0.3	0.2	0.1	0.6	0.6	0.9	0.0	0.0	0.0
C16:0	12.3	12.6	12.4	12.6	12.3	11.9	11.8	11.9	12.2	11.9	11.7	13.9	14.0	16.0	18.3	14.1	16.2	16.2	16.0	13.7	14.0	14.1	19.2	12.1	12.2
C16:1	0.4	0.6	0.6	0.6	0.9	1.0	1.1	1.1	0.5	0.4	0.5	3.0	3.4	3.1	3.0	3.1	3.2	3.7	4.0	3.3	3.2	4.1	1.8	1.3	0.7
C17:0	0.1	0.2	0.2	0.2	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.5	0.6	0.6	0.7	0.6	0.7	0.7	0.7	0.6	0.7	0.6	0.6	0.2	0.3
C17:1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.3	0.4	0.3	0.3	0.3	0.4	0.3	0.2	0.3	0.4	0.4	0.3	0.2	0.3
C18:0	2.3	2.4	2.3	2.3	2.8	2.9	3.0	3.1	2.3	2.1	1.9	2.8	2.9	3.9	4.9	3.1	3.2	3.4	2.6	3.3	2.9	2.5	2.6	3.1	1.8
C18:1	30.7	30.1	29.3	28.6	54.3	59.3	63.2	65.2	30.3	28.1	25.1	12.7	12.5	12.4	15.8	27.1	31.9	44.3	54.5	14.2	12.9	13.0	27.6	67.2	19.6
C18:2	47.7	44.5	42.8	37.8	24.4	20.0	16.2	13.8	46.1	46.9	47.3	9.6	6.9	5.5	12.8	9.4	9.8	12.3	14.6	9.4	9.5	7.7	12.7	13.2	52.5
C18:3 γ	1.1	1.2	1.3	1.3	0.9	0.8	0.8	0.8	1.5	1.7	1.8	0.2	0.2	0.2	0.4	0.3	0.4	0.4	0.4	0.4	0.3	0.2	2.4	0.9	3.3
C18:3 α	3.7	5.0	5.6	7.5	2.3	2.0	1.8	1.7	3.9	4.2	4.6	2.7	3.3	4.3	3.7	4.1	5.2	3.5	2.9	1.8	2.6	1.3	28.8	1.8	8.0
C20:1	0.3	0.3	0.3	0.5	0.1	0.1	0.1	0.1	0.3	0.3	0.2	0.4	0.3	0.2	0.1	0.4	0.2	0.2	0.1	0.1	0.3	0.1	0.0	0.0	0.0
C20:2	0.0	0.3	0.5	0.9	0.4	0.4	0.4	0.5	0.3	0.4	0.6	0.2	0.4	0.6	0.4	0.6	0.5	0.6	0.2	0.2	0.2	0.3	0.0	0.0	0.0
C22:0	0.3	0.3	0.4	0.5	0.3	0.3	0.3	0.3	0.6	0.9	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C20:4	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.2	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C22:1	0.1	0.2	0.4	0.6	0.3	0.3	0.4	0.4	0.2	0.3	0.6	0.0	0.0	0.0	0.0	0.2	0.1	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0
C20:5	0.1	0.7	1.2	2.3	0.1	0.1	0.1	0.0	0.2	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C24:0	0.6	0.4	0.6	0.7	0.3	0.3	0.2	0.2	0.6	0.6	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C24:1	0.0	0.1	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C22:5	0.0	0.5	0.9	1.9	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
C22:6	0.0	0.0	0.1	0.3	0.2	0.2	0.2	0.2	0.4	0.7	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SFA	15.9	16.3	16.5	17.1	15.8	15.5	15.6	15.7	16.2	15.9	16.7	70.6	72	72.8	62.8	54.2	48	34.3	22.7	69.8	70	72	26.4	15.5	15.6
MUFA	31.6	31.4	30.9	30.8	55.7	60.8	64.9	67	31.4	29.3	26.7	16.7	17.1	16.4	19.7	31.4	36.1	48.9	59.2	18.5	17.4	18.5	29.3	68.4	20.3
PUFA	52.6	52.2	52.5	52.2	28.3	23.5	19.5	17	52.7	54.6	56.5	12.7	10.8	10.6	17.3	14.4	15.9	16.8	18.1	11.8	12.6	9.5	43.9	15.9	63.8

acid and SFA contents of the larvae ($p < 0.001$), hence, the highest MUFA and PUFA contents of BSFL. These relationships were especially relevant in case of OP-diets. Thus, strong linear relationships were found between the content of lauric acid of the larvae and the proteins ($r = 0.985$, $p = 0.002$) and carbohydrates ($r = 0.973$, $p = 0.005$) of the diets, as well as negatively for lipids ($r = -0.996$, $p < 0.001$) and fibers ($r = -0.995$, $p < 0.001$) of the diets. An illustration of these relationships between nutrients of the diets and the lauric acid accumulation in larvae is shown in Fig. 5 (A-D).

Besides the amount of lipids of the diets, the specific fatty acid profile of such dietary lipids should be strongly considered on the impact on the fatty acid profile of the larvae. In this sense, it was interestingly found that those major fatty acids of the diets that negatively impacted on the lauric and SFA accumulation of the larvae were oleic and stearic acids ($p < 0.001$); whereas those dietary fatty acids that positively favoured the accumulation of lauric acid and SFA were the major PUFA, linoleic acid and linolenic acid ($p < 0.05$). Again, these relationships were especially relevant in case of OP-diets. Thus, strong negative linear relationships were found between the content of lauric acid of the larvae and oleic acid ($r = -0.905$, $p = 0.035$) and stearic acid ($r = -0.934$, $p = 0.020$) of the diets, whereas strong positive linear relationships were found for linoleic acid ($r = 0.906$, $p = 0.034$) and linolenic acid ($r = 0.896$, $p =$

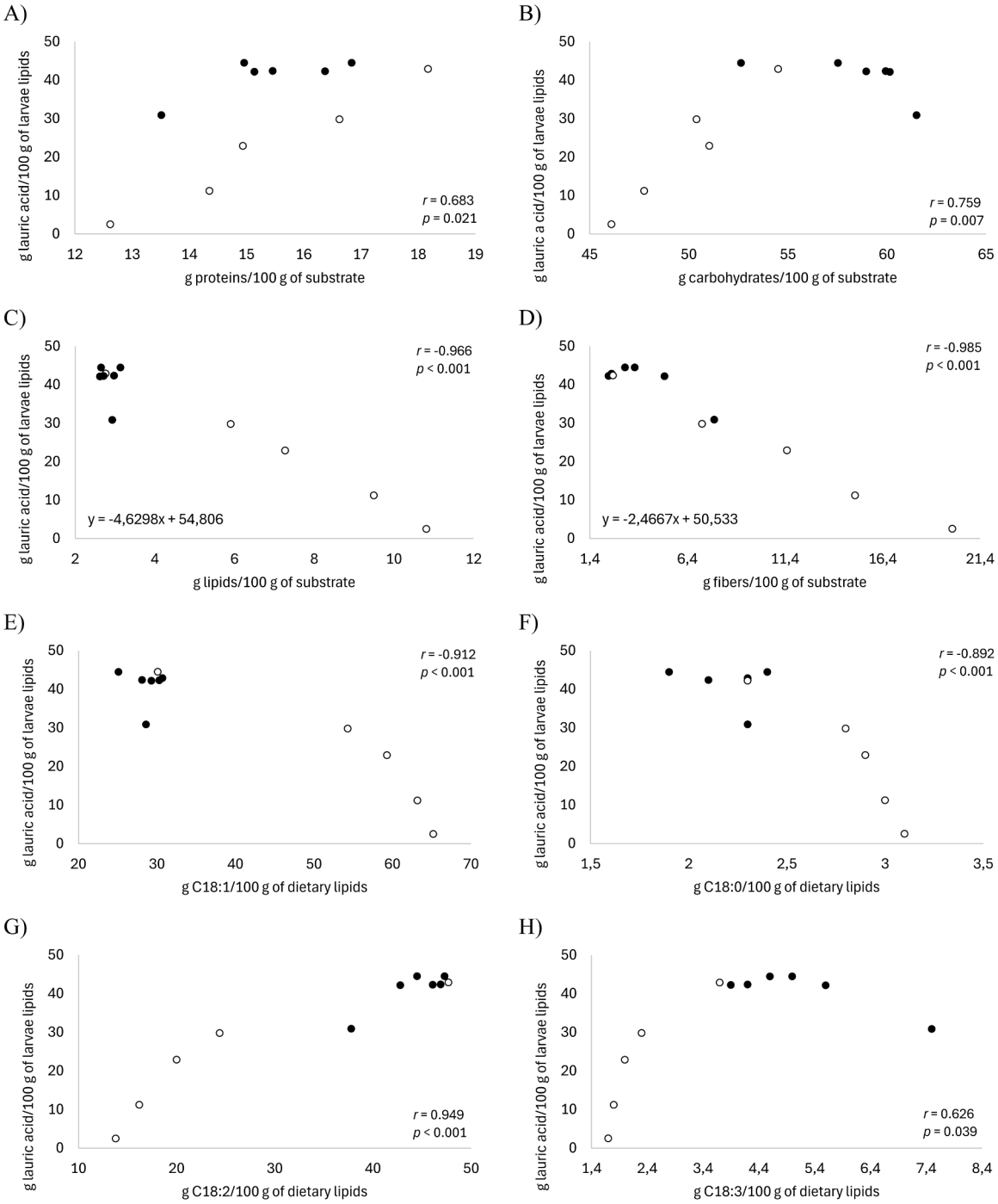

Fig. 5. Relationship between the nutritive composition (A-D), or between the major fatty acids (E-H) of the substrates of BSFL, and the subsequent lauric acid content of the fed larvae. White dots correspond to control and OP-based diets (0 %, 30 %, 50 %, 70 %, 90 %), while black dots correspond to OL or QH based diets. Values of Pearson's test for the total represented values are shown. For those strong linear relationships ($R^2 > 0.9$), the equation is included.

0.040). These relationships for the major fatty acids of the diets and lauric acid accumulation are shown in Fig. 5 (E-H).

It should be remarked that these general effects caused on lauric acid accumulation were also significantly found for the accumulation of the saturated myristic acid ($p < 0.05$). All these results would agree with the previous described hypothesis for BSFL that the PUFA may synthesize SFA via β-oxidation reaction acetyl CoA and that BSFL accumulate these PUFA up to almost 15 % but are finally metabolized to synthetize SFA as lauric acid (Hoc et al., 2020). However, it should be also remarked that these impacts of the dietary fatty acids on major SFA of BSFL (lauric acid and myristic acid) did not impact on the other major SFA of BSFL, palmitic acid. This would be in agreement with the theory that a great amount of palmitic acid of BSFL is related to biosynthesis instead of simple accumulation from diet (Hoc et al., 2020).

Therefore, the present study shows, according to Fitriana et al. (2022), that the fatty acids of BSFL are complex components that can be modified by the amount of specific macronutrients of the substrate, the specific fatty acid profile of diets, as well as the combined action of these factors with the subsequent endogenous lipid metabolism due to the action of diverse desaturase enzymes. Further studies are still needed to clearly understand the lipid metabolism of BSFL and the complex impact of the diets.

The obtained results for OP-based diets in the current study are of great interest, since one of the remarked problems of the lipids from BSFL for being used for food and feed is the SFA profile. Although it is a topic that has not been still clearly concluded, it seems that BSFL fats are not the most adequate for animal feeding with requirements of unsaturated diets or especially polyunsaturated diets (Raes et al., 2004; Tocher, 2015). This is the case of aquaculture, which is currently the major livestock of interest for alternative diets as insect feeds, including BSFL (Mohan et al., 2022). Therefore, additional defatting steps are being performed to remove the fat from the insect meals (Hurtado-Ribeira et al., 2023b). In this sense, obtaining a totally different unsaturated profile for BSFL as obtained in this study, more friendly to be used for animal feeding, by using strategies of diet intervention as olive pomace, would be a relevant strategy to reach a simultaneous double aim of: 1) favouring the use of BSFL in animal feeding without the defatting step and 2) valorising the problematic olive pomace by-product. Nevertheless, despite this promising solution, it should be remembered that the highest olive pomace levels of inclusion in the diets of BSFL in the current study were not adequate for a proper growth of the larvae, and only values up to 50 % would be admissible without compromising the larvae production. Despite this limitation, the lipids of the OP50 larvae would still be also of great interest, showing also an attractive improvement on the fatty acid composition respect to the control larvae (decrease of SFA from 71 % to 48 %; increase of MUFA from 17 % to 36 % and increase of PUFA from 13 % to 16 %). These larvae mainly contained oleic acid (32 %) as major fatty acid, followed by lauric acid (23 %), palmitic acid (16 %) and linoleic acid (10 %).

Conclusions

The feeding of BSFL with olive leaves up to 15 %, full-fat dry olive pomace up to 50 %, and quinoa husk, up to 50 %, allow the successful bioconversion of such by-products, along with an adequate development and growth of BSFL. These diets do not impact on the macronutrients of the larvae, but contain more chitin. Additionally, the larvae from the selected level of olive pomace up to 50 % contain a much more desirable unsaturated fatty acid profile.

The nutritional and balanced composition of the tested substrates is determinant for the efficient growth of BSFL and the later composition of the larvae. Specifically, high levels of olive leave are not adequate due to unbalanced low protein, high carbohydrates and high fiber of the substrates. On the contrary, high levels of full-fat dry olive pomace are unbalance on high lipid and fiber, and low carbohydrate. As consequence, these larvae are lower in protein and ashes, and higher in lipids and chitin. The similar nutritional composition of quinoa husk to conventional diets produces quite similar larvae.

The unbalanced diets are also involved on a modification of the fatty acid profile of the larvae, especially remarkable in case of olive pomace. Thus, high levels of dietary carbohydrates and proteins favour the typical saturated profile of BSFL, whereas high levels of dietary lipids and fiber modify the lipids of BSFL to a more unsaturated one. Furthermore, the major fatty acids of olive pomace, as oleic acid and linoleic acid, seem to be determinant on the saturated profile of the larvae, both limiting or favouring the accumulation of the major lauric acid, respectively.

Finally, the potential impact of specific minor molecules of the experimental tested by-products on growth parameters, nutritional composition and fatty acid profile of BSFL cannot be ruled out. In fact, a negative impact of increasing dietary phenolic compounds on the growth of the larvae was preliminary evidenced.

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Ethical statement

-No applicable ethical issues for insects.
-No human study.

CRediT authorship contribution statement

Esther Rodríguez-González: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **María D. Hernández-Llorente:** Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luis Vázquez:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Fernando G. Barroso:** Writing – review & editing, Conceptualization. **María J. Sánchez-Muros:** Writing – review & editing, Conceptualization. **Agnes T. Varga:** Methodology, Data curation. **Tiziana Fornari:** Visualization, Conceptualization. **Mónica R. García-Risco:** Writing – review & editing, Visualization, Supervision, Data curation. **Diana Martin:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.fufo.2025.100718.

Data availability

Data will be made available on request.

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