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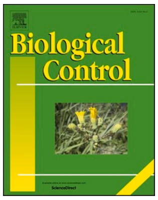

Dynamic intraguild interactions between two sympatric and congeneric coccinellid species associated with aphids could explain their coexistence in citrus agroecosystems

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HIGHLIGHTS

- The two prevalent citrus coccinellid species engage in intricate Intraguild interactions.
- IGI patterns vary influenced by factors such as prey density and quality.
- The dynamic nature of IGI may explain changes on their relative dominance.
- The dynamic nature of IGI prompts a seasonal niche partitioning.
- This phenomenon would contribute to the coexistence of the two coccinellid species.

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ABSTRACT

Scymnus interruptus and *Scymnus subvillosus* (Coleoptera: Coccinellidae) are the most frequent aphid predators in Western Mediterranean citrus agroecosystems. Intraguild predation (IGP) between them would be expected, but how IGP might affect their coexistence and biological control function remains unknown. In this work, we assess the frequency of predator encounters in the field and investigate intraguild predation between these two predators in laboratory settings. Different field prey scenarios derived from the field observations were simulated with the two dominant aphid species in this agroecosystem, *Aphis gossypii* and *Aphis spiraecola*.

Scymnus subvillosus and *S. interruptus* engaged in IGP but the magnitude and symmetry varied with the prey species and abundance. At high aphid densities, IGP was symmetric and weak, whereas, at low aphid densities, IGP was strong and very asymmetric, with *S. interruptus* taking the role of the intraguild predator. The developmental time of *S. subvillosus* was reduced when competing with *S. interruptus* at high extraguild prey densities. The adult size of both predators under weak IGP also increased even when the developmental time had been reduced.

We predict that high aphid infestations in the spring would benefit *S. subvillosus,* while the strong and asymmetric IGP at low aphid infestations would hinder its coexistence with *S. interruptus*. Our results give a theoretical explanation to what is observed in the field: *S. subvillosus* is typically dominant during the high aphid infestations of the spring, whereas *S. interruptus* increases in relative dominance during the summer and fall when aphid abundance is much less.

1. Introduction

Aphid predatory feeding guilds are diverse and abundant, with known representatives of numerous families such as Cecidomyiidae, Chrysopidae, Coccinellidae, Miridae and Syrphidae (Hemptinne et al., 2000; Van Veen et al., 2008; Bouvet et al., 2019a, 2021). Colonies are restricted to specific periods of the season and outbreaks are followed by significant population declines. Intraguild interactions among the components of these predatory guilds are, therefore, particularly likely (Lucas, 2005).

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The interaction between two predators that share and compete for the same food resource is frequently resolved by one preying on the other [intraguild predation (IGP)]. IGP significantly modulates the topology of food webs and community structure (Polis and Holt, 1992; Müller and Brodeur, 2002; Arim and Marquet, 2004). This often leads to a reduction in top-down control, relaxing predation pressure on the shared resource species and consequently increasing its biomass. In agroecosystems, comprehending these ubiquitous interactions holds potential for enhancing the interpretation of biological control mechanisms orchestrated by predatory guilds. The intensity (frequency of the event) and symmetry (direction of the interaction) of IGP hinge on the specific biological and ecological attributes of the three participants: the intraguild predator (IGpredator), intraguild prey (IGprey) and the shared food resource [extraguild prey (EGprey)] (Polis et al., 1989; Rosenheim et al., 1995; Lucas, 2005; Montserrat et al., 2012). Voracity, aggressiveness, degree of polyphagy, shared resource exploitation efficiency, mobility, size and developmental stage of both IGpredator and IGprey shape the outcome of IGP, while the abundance and quality of the EGprey may exert a determining influence (Lucas et al., 1998; Arim and Marquet, 2004; Royer et al., 2024). Given the dynamic nature of these traits, IGP emerges as a multifaceted interaction within ecological systems. Beyond the lethal effects of IGP, interactions between predators exploiting the same food resource, such as exploitation and interference competition, also encompass nonconsumptive effects (NCEs) that influence prey behavior, development, and physiology. Under this type of interactions, predators adapt their biology and ecology to accommodate more stressed conditions (Michaud et al., 2016). NCEs can drive shifts in population dynamics and community structure, sometimes surpassing the impact of lethal consumptive effects (Werner and Peacor, 2003; Bayoumy and Ramadan, 2018; Bayoumy et al., 2018).

Coccinellids represent a pivotal component of aphidophagous guilds. These predators have been recorded from a wide range of habitats and preying on many different species of aphids. Multi-specific coccinellid assemblages frequently converge on single aphid patches, increasing the likelihood of different types of intraguild interactions among these predators (Agarwala and Ghosh, 1988; Evans, 1991; Bouvet et al., 2020).

Mediterranean citrus agroecosystems frequently experience economically damaging outbreaks of *Aphis gossypii* Glover and *Aphis spiraecola* Patch (Hemiptera: Aphididae) during the spring citrus flushing period (Hermoso de Mendoza et al., 2001, 2006; Bouvet et al., 2019a). Coccinellids are the most important group of predators associated with these aphid species in terms of abundance and number of species (Bouvet et al., 2019a, 2020). *Scymnus subvillosus* Goeze and *Scymnus interruptus* Goeze (Coleoptera: Coccinellidae) frequently dominate citrus aphidophagous guilds. These two coccinellid species have the ability to effectively curtail aphid outbreaks in citrus by targeting colonies in their earlier phenological stages (Gómez-Marco et al., 2016; Bouvet et al., 2019a, 2020). However, under the current pest management strategies, biological control often falls short in maintaining aphid populations below their economic injury levels (Bouvet et al., 2019a; Urbaneja et al., 2020).

Scymnus subvillosus and *S. interrutus* coexist in Mediterranean citrus agroecosystems throughout the season. While *S. subvillosus* was found to be dominant during the high aphid infestation of spring, *S. interruptus* gained relative dominance later in summer and fall when aphid abundance is less (Bouvet et al., 2019a, b, c). During the spring major flushing period, juvenile stages are expected to be found sharing the same aphid patches. The probability that juveniles of one of the two coccinellid species attack the other one (IGP) or even that both species attack each other (reciprocal IGP) is therefore also expected to be high. Model-based predictions suggest that IGP significantly dampens the probability of coexistence, potentially leading to the displacement of at least one competitor (Montserrat et al., 2012; Schellekens and van Kooten, 2012). However, this phenomenon is less frequently observed in natural and semi-natural systems where predator coexistence prevails.

By delving into the study of consumptive and NCEs effects resulting from the intraguild interactions between *S. subvillosus* and *S. interruptus,* alongside their EGprey preferences (Bouvet et al., 2019b), we seek to gain a deeper understanding of the syntonic and stable coexistence of these two key aphid predators. This comprehension holds potential for advancing more efficient conservation biological control strategies against *A. gossypii* and *A. spiraecola* in citrus agroecosystems. We propose that the coexistence of the two *Scymnus* species is likely facilitated by the occurrence of low-frequency and non-reciprocal IGP when sharing the same food patches. Given the expected diversity of scenarios in which these predators may co-occur, our study aims to characterize the dynamics of IGP between *S. interruptus* and *S. subvillosus* through laboratory simulation of six combinations of EGprey availability commonly observed in the study agroecosystem (Bouvet et al., 2019a, b): i) high and ii) low EGprey densities with aphid patches dominated by *a*) *A. spiraecola*, *b*) *A. gossypii* and *c*) the combination of both *A. spiraecola* and *A. gossypii.*

2. Material and methods

2.1. Field evaluations

To gain a deeper understanding of the circumstances under which intraguild interactions between *S. subvillosus* and *S. interruptus* are given under field conditions, the presence of larvae from both coccinellid species within aphid colonies on citrus shoots was assessed during the major spring citrus flushing period (Bouvet et al., 2020). The study was conducted over five consecutive weeks in four commercial citrus clementine groves under organic management—Moncada, Algimia, and Castellon (from April 14 to May 19, 2015), and Moncada, Ribesalbes, and Castellón (from April 7 to May 25, 2016). In each orchard and on each sampling date, five shoots infested with aphid colonies at the same phenological stage (one from each canopy orientation and one from inside the canopy) from 20 randomly selected trees, resulting in a total of 100 shoots per orchard and sampling date, were collected. Subsequently, the shoots were examined under a stereoscope, and the number of aphids per shoot as well as their developmental stage, was recorded. All aphid specimens were taxonomically identified to the species level. Similarly, the count of *S. subvillosus* and *S. interruptus* larvae on each shoot was also documented. Shoots were later classified according to *i)* the aphid species conforming the colonies (shoots hosting monospecific *A. spiraecola* colonies, shoots hosting monospecific *A. gossypii* colonies, and shoots hosting mixed colonies of the two aphid species), *ii)* the presence or not of larvae of any of the two coccinellid species (shoots with *S. subvillosus*, shoots with *S. interrupuls*, shoots with both *Scymnus* species together, and shoots without the presence of larvae), and *iii)* the amount of aphids available for the predators (shoots hosting incipient colonies with less than twice the daily prey quantity necessary for the immature predator development, 12 aphids per predator; shoots hosting aphid colonies with more than twice the daily prey quantity necessary for the immature predator development).

2.2. Stock cultures

Laboratory colonies of *A. spiraecola* and *A. gossypii* were initiated in spring 2014 by collecting specimens on clementine trees [*Citrus clementina* Hort. Tan. (Geraniales: Rutaceae)] in orchards belonging to the Valencian Institute of Agricultural Research (IVIA) in Moncada, Valencia, Spain (39°35′17.43″N / 0°23′53.28″O). Aphids were reared on two-year-old, potted, clementine plants (*Citrus reticulata* Blanco [Clementina de Nules cultivar Iniasel 22] grafted onto *Citrange* Carrizo rootstock [*Poncirus trifoliata* (L.) Rafinesque-Schmaltz × *Citrus sinensis* (L.) Osbeck]) and kept in a climate-controlled chamber of a glasshouse at 24 ± 2 °C, 60 ± 5 % relative humidity under natural photoperiod.

Myzus persicae (Sulzer) (Hemiptera: Aphididae) (green phenotype) was reared on sweet pepper plants (*Capsicum annuum* L.; Solanales:

Solanaceae) and initiated from a stock colony maintained on potted broad bean plants (*Vicia faba* L.; Fabales: Fabaceae) at IVIA since 2004. The rearing system on sweet pepper plants was chosen as it facilitates easy manipulation of the aphids. The colony was kept at the same rearing conditions described for *A. spiraecola* and *A. gossypii*.

Colonies of the two predatory coccinellids, *Scymnus subvillosus* and *S. interruptus*, were established also in the spring of 2014, by beat-tray sampling from within the IVIA clementine orchards mentioned above to collect adult specimens (n = 200 per species). Adult specimens of each coccinellid species were kept in Petri dishes, 9.0 cm in diameter by 1.5 cm in height (n = 50 per Petri dish). The lid of the dish was adapted with a muslin-covered hole (4 × 4 cm) to facilitate gas exchange and avoid humidity saturation. In each Petri dish, pepper leaves highly infested with *M. persicae* were provided every two days. Pollen and honey were also supplied as supplementary food for the predators. Water was offered on filter paper. Petri dishes were kept in a growth chamber (SANYO MLR-350; Sanyo, Japan) at 25 ± 1° C, 60–70 % RH and 14:10 h (L:D) photoperiod. Every two days, eggs of each coccinellid species were carefully selected from the rearing units and individually placed in Petri dishes measuring 5.5 cm in diameter and 1.0 cm in height. The Petri dishes featured a muslin-covered hole (2 × 2 cm) in the lid to facilitate gas exchange. A plaster ball (5 mm) was also positioned at the base to maintain consistent humidity levels within the experimental units. Emerged larvae were further used for the experiments.

2.3. Intraguild studies

The effects of the intraguild interactions between the two coccinellid species (*Scymnus interruptus* and *S. subvillosus*) on their immature survival, immature developmental time, and adult size, were studied by pairing two first instar larvae (<24 h old), one of each species (n = 172 pairs of predators) in Petri dishes (5.5 cm in diameter × 1.0 cm height) adapted for gas exchange, as explained above. The bottom of the dishes was covered with a layer of plaster that was moistened daily to keep a constant humidity inside the experimental arena. Three different EGprey diets were offered to the predators: *a*) *A. spiraecola*, *b*) *A. gossypii* and *c*) a mixed diet of *A. spiraecola* and *A. gossypii* (1:1). Each diet was offered daily at two densities: *i*) Low EGprey density (LD): half of the estimated quantity of prey required daily for the immature predator development (3 adult aphids/predator; i.e., 6 adult aphids per experimental arena and each pair of predators, at the onset of the experiment) (Tawflk *et al.,* 1973; Sebastião et al., 2015) and *ii*) High EGprey density (HD): twice the daily prey quantity necessary for the immature predator development (12 adult aphids/predator; i.e., 24 adult aphids per experimental arena and each pair of predators, at the onset of the experiment). Diet was adjusted to maintain the per capital food level when larvae mortality was given. Each pair of immature predators from each of the six treatments (3 diets under 2 prey densities) were checked daily under a stereo microscope until death or adult emergence. The developmental stage of each predator (L1, L2, L3, L4, prepupa and pupa) and whether they were alive or dead were recorded (Bouvet et al., 2019b). After adult emergence, specimens were sexed and photographed using a camera-mounted stereo microscope to measure their length and width with the Leica 148 Application Suite (v4.6.2). Control treatments consisting of single individuals of *S. interruptus* (n = 81) and *S. subvillousus* (n = 82) in each experimental arena were also set with identical EGprey diets and densities. Three additional experimental arenas with the three different EGprey (n = 24 aphids) but without the predators were also set to check the daily natural mortality of the EGprey. All experimental arenas were kept in two growth chambers under the same conditions described above.

2.4. Data analyses

In the field evaluations, the observed frequency of each type of aphid colony found in the sampled citrus shoots was compared to a theoretical expectation of equal frequencies using a Chi-square test of goodness-of-fit. The frequency with which each *Scymnus* species was singly found in the shoots as well as the frequency of co-occurrence of the two species in the same shoot was also compared to a theoretical expectation of equal frequencies using an Exact test of goodness-of-fit since the number of observations (shoots with the presence of *Scymnus* larvae) was less than a thousand (McDonald, 2014). The frequency of association of larvae of each *Scymnus* species to each type of aphid colony and the frequency of association of co-occurring larvae of the two *Scymnus* species to each type of aphid colony was also studied using Exact tests.

In the laboratory studies, the effect of predator species, EGprey density, EGprey diet and the co-occurrence or not of the two predators on their mortality from L1 to adult was studied using generalized linear model (GLM) analysis (Wolfinger and O'connell, 1993). A binomial error distribution of the response variable (predator mortality) was selected. Predator species (species), EGprey density, EGprey diet and co-occurrence or not of the two predators (intraguild interaction [IGI]) were used as explanatory variables. All interactions between the explanatory variables were initially included in the model. Those fixed factors and interactions without a significant effect in the full model were sequentially excluded. Model selection between the full and reduced models was made on the Akaike (AIC) information criterion (Anderson and Burnham, 2002). Least square means differences were used to check mortality differences between the two predator species when they were coexisting or not in the same arena and under the different EGprey diets, and EGprey density combinations.

IGP symmetry between the two predator species was evaluated by comparing the number of cases in which one of the two predators killed the other, to a theoretical index corresponding to a symmetric interaction (1:1) (Lucas et al., 1998). An exact binomial test of goodness-of-fit was used. Intraguild predation intensity was assessed as the number of cases in which no predator was killed with respect to the total number of at the beginning of the experiment.

Mortality attributed to intraguild interactions was estimated for each immature developmental stage of *S. interruptus* and *S. subvillosus* at both high (HD) and low (LD) EGprey densities by correcting the predator mortality in the predator coexisting treatments with that obtained in the control treatments, using the Henderson and Tilton formula (Henderson and Tilton, 1955; Monzó et al., 2014). No EGprey diet differentiation was made since no significant effects of this factor (diet) on predator mortality were found in the first analysis of the study.

Two NCEs of the intraguild interactions between the two predators were also studied: effects on *i*) the developmental time of immature predators and *ii*) the subsequent size of the emerged adults.

The effects on the developmental time of immatures (from egg eclosion to adult emergence) were studied using generalized linear model (GLM) analysis. Immature developmental time was the dependent variable, and predator species (species), EGprey density, EGprey diet, and the co-occurrence or not of the two predators in the same arena (IGI) were used as explanatory variables. All interactions between the explanatory variables were included in the full model. Model selection between the full and reduced models was done following the same criteria as explained above. Different error distributions of the response variable were tested. The normal distribution was selected since its ratio of the Pearson Chi-Square to its degrees of freedom was the closest to 1 (Schabenberger and Pierce, 2001). Least square means differences were used to check mortality differences between predators coexisting or not in the same arena, for each predator, EGprey diet, and EGprey density combination.

The effect of juvenile intraguild interactions on the size of adults was studied using GLM analysis. Adult size (enclosed area of an ellipse = $\pi \cdot a \cdot b$, were a and b are the lengths of the semi-major and semi-minor axes in mm^2) was used as the response variable and predator species (species), EGprey density, EGprey diet, and the co-occurrence or not of the two predators (IGI) were used as explanatory variables. Because males and females of the two coccinellid species have different sizes

(Bouvet et al., 2019b), gender (male, female) was also included as an explanatory variable. All interactions involving IGI were included in the model. Model selection between the full and reduced models was done. Normal error distribution of the response variable was selected following the same criteria as explained above. Post hoc *t*-test (Tukey) comparisons were used to study differences in adult size between predators that share the same arena at low and high prey densities and those from the control treatment at high prey densities.

Kenward and Roger Satterthwaite's approximation for degrees of freedom was included in all the GLMM models of this study (Kenward and Roger, 1997).

All the analyses were done using SAS ® University Edition software.

3. Results

3.1. Field evaluations

During the field study, 2,994 aphid-infested citrus shoots were examined. Shoots hosting monospecific *A. spiraecola* colonies were predominant (*Chi-square* = 11.02; df = 2; $P < 0.0001$), accounting for 58.3 % of the total shoots. Following this, shoots hosting mixed colonies of both *A. gossypii* and *A. spiraecola* species constituted 17.1 %, while shoots with monospecific colonies of *A. gossypii* represented 15.5 % of the shoots, both types of colonies found with similar frequencies (*Chi-square* = 24.58; df = 1; $P = 0.117$) (Table 1). A smaller subset of shoots (9.1 %) contained remnants of predated colonies, making it impossible to discern the original aphid species composition.

The presence of *Scymnus* larvae was noted in 207 shoots (6.9 %), with both *Scymnus* species occurring in similar frequencies (*Exact Test*: df = 1; $P = 0.6988$). In shoots where these predators were observed, *S. subvillosus* was the sole coccinellid species in 41.5 % of cases, while *S. interruptus* was the only coccinellid in 39.1 %. In a lesser proportion (*Exact Test*: df = 2; $P = 0.0002$), larvae of both species were found in the same shoot sharing the same food resource (19.3 % of the shoots with *Scymnus* presence).

Larvae of *S. subvillosus* were predominantly associated with *A. spiraecola* colonies (94.2 %) (*Exact Test*: df = 3; $P < 0.0001$), whereas *S. interruptus* larvae were mainly linked to *A. spiraecola* colonies (60.5 %) and, to a lesser extent, mixed colonies of the two aphid species (29.6 %) *Exact Test*: df = 1; $P < 0.0001$) (Table 1). Larval coexistence of the two *Scymnus* species in the same shoot was equally associated with *A. spiraecola* colonies (22.5 %) and mixed colonies (17.5 %) (*Exact Test*: df = 1; $P = 0.8036$). However, the majority of shoots where larvae of both *Scymnus* species coexisted had previously predated aphid colonies, and the original species composition remained unclear (57.5 % of cases) (*Exact Test*: df = 3; $P < 0.0001$).

Of the 40 shoots where both *Scymnus* species coexisted, 37 had one larva of each coccinellid species, while in the remaining three shoots, two larvae of *S. subvillosus* coexisted with one larva of *S. interruptus*. Out of the 831 shoots hosting young aphid colonies with fewer than 12 individuals per predator, 10 also had *Scymnus* larvae— two hosting a sole *S. subvillosus* larva, three hosting a *S. interruptus* larva, and five hosting together one larva of each *Scymnus* species.

Table 1

Aphid patch composition (type of aphid colony and *Scymnus* species present in each patch) of citrus shoots collected during the spring flushing period of two consecutive seasons in four organic commercial citrus groves.

	Sampled shoots	**Presence of predators**		
		S. subvillousus	*S. interruptus*	*S. interruptus* + *S. subvillous*
Aphis spiraecola colony	1746	81	49	9
Mixed aphid colony	513	1	24	7
Aphis gossypii colony	464	3	6	1
Predated colony	271	1	2	23
Total	**2994**	**86**	**81**	**40**

3.2. Predator mortality

Predator mortality from L1 to the adult stage was higher for *S. subvillosus* than for *S. interruptus* (species: $F = 38.26$; df = 1, 499; $P < 0.0001$). Mortality was higher when the two predators shared the same arena and EGprey (IGI: $F = 19.93$; df = 1, 499; $P < 0.0001$) and mainly at low prey densities (EGprey density: $F = 38.20$; df = 1, 499; $P < 0.0001$) (Table 2). No diet effects were observed on predator mortality (Diet: $F = 2.09$; df = 2, 483; $P = 0.1254$). The effect of the co-occurrence of the two predator species in the same arena on their mortality was different for each species (species × IGI: $F = 14.03$; df = 1, 499; $P = 0.0008$). Predator co-occurrence notably increased the mortality of *S. subvillosus* ($t = -5.51$; df = 499; Adjusted $P < 0.0001$). Nevertheless, increased mortality was not observed for *S. interruptus* ($t = -0.54$; df = 499; Adjusted $P = 0.5904$). The effect of the EGprey density on the mortality of the predators was different between the two *Scymnus* species (species × EGprey density: $F = 10.84$; df = 1, 499; $P = 0.0011$). Mortality at low EGprey densities was higher than at high EGprey densities in *S. subvillosus* ($t = -3.11$; df = 499; Adjusted $P = 0.041$), but this effect was not so evident for *S. interruptus* ($t = -2.89$; df = 499; Adjusted $P = 0.077$) (Table 2). When the two predators shared the arena (predator co-occurrence), the differences in mortality between predators were even higher and dependent on the EGprey density (species × IGI × Egprey density: $F = 13.69$; df = 1, 499; $P = 0.0002$). The percentage of *S. subvillosus* mortality at low Egprey densities and under intraguild interactions was over 95 %, whereas it barely reached 20 % for *S. interruptus* ($t = -5.53$; df = 499; Adjusted $P < 0.001$). At high Egprey densities, mortality of *S. subvillosus* was nevertheless not statistically different from that of *S. interruptus* ($t = -2.48$; df = 499; Adjusted $P = 0.206$).

3.3. Intraguild predation symmetry and intensity

IGP was symmetric at high Egprey density for the three Egprey diets (*A. spiraecola*: $P = 0.35$; *A. gossypii*: $P = 0.10$; mixed diet: $P = 1.00$). At this Egprey density, the least intense IGP was observed when the Egprey mixed diet (*A. spiraecola* + *A. gossypii*) was offered to the predators. In that treatment, the two predators reached the adult stage in 18 of the 24 replicates (Fig. 1**A**). Intraguild predation was nevertheless strong and markedly asymmetric, favoring *S. interruptus* at low Egprey density and with the three Egprey diets (*A. spiraecola*: $P < 0.01$; *A. gossypii*: $P < 0.01$; mixed diet: $P < 0.01$). At low Egprey density, in all the replicates, at least one of the two predators died before reaching the adult stage (Fig. 1**B**).

Table 2

Percentage of mortality (mean ± SE) of *Scymnus subvillosus* and *S. interruptus* from L1 to adult stages under two densities of extraguild prey (high aphid densitiy [HD] and low aphid density [LD]) and either under predator co-occurrence (IGI) or predator alone (control). The number of replications for each treatment combination is displayed within the brackets. For each predator species and EGprey density combination, significant differences in mortality between predators under IGI and predators without IGI (control) are indicated with one asterisk ($P < 0.05$) (LS-means differences).

EGprey density/IGI	**Mortality (%)**	
	S. interruptus	*S. subvillosus*
HD-IGI	**25.3 ± 4.6* (91)**	**42.9 ± 5.2* (91)**
HD-control	**9.1 ± 4.3* (44)**	**17.8 ± 5.7* (45)**
LD-IGI	21.0 ± 4.5 (81)	**96.3 ± 2.1* (81)**
LD-control	37.8 ± 8.0 (37)	**51.4 ± 8.3* (37)**

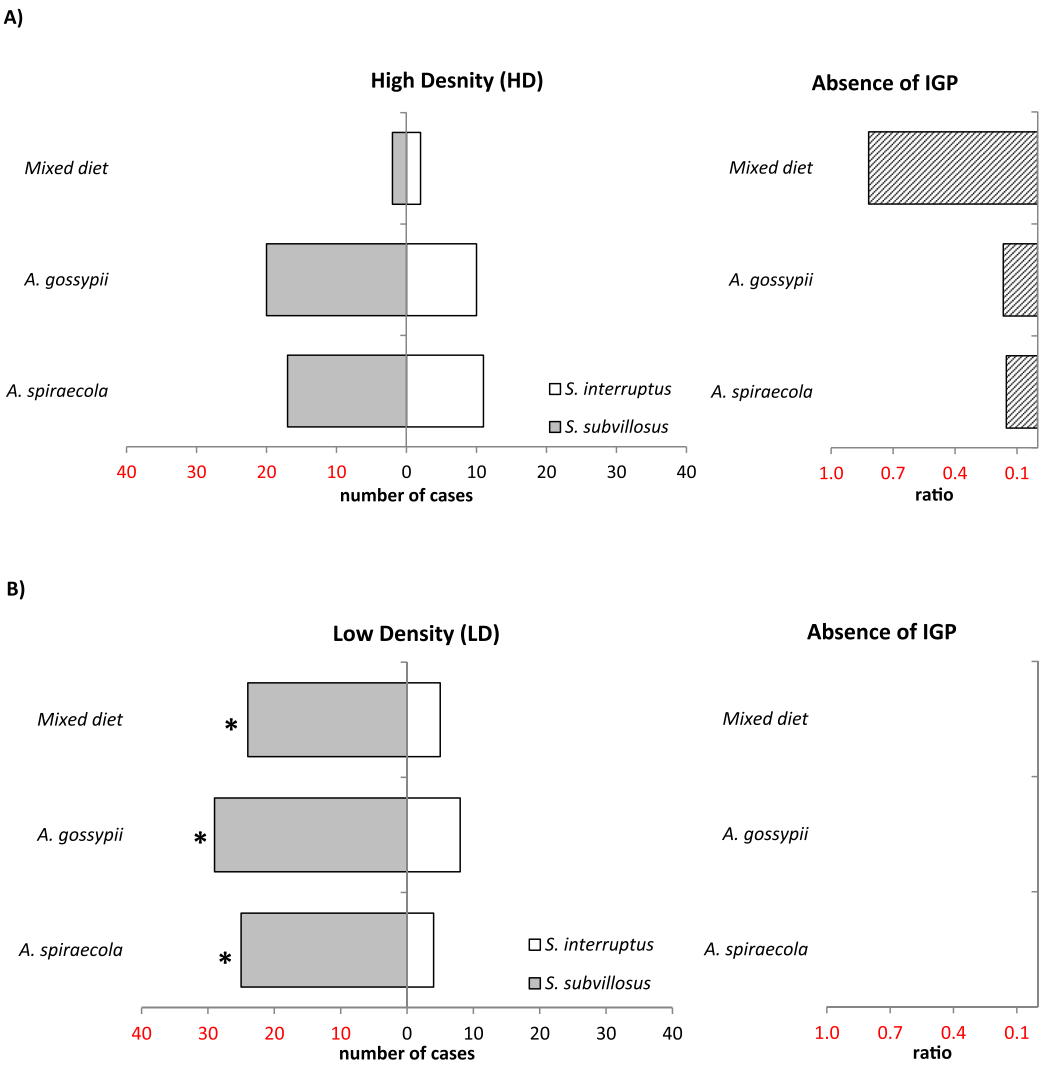

Fig. 1. Intraguild predation symmetry and intensity (number of cases in which the predator died before reaching the adult stage) of *S. interruptus* and *S. subvillosus* sharing the same EGprey patch at **A)** high and **B)** low EGprey densities and with three EGprey diets: *A. spiraecola*, *A. gossypii* and mixed diet (*A. spiraecola* + *A. gossypii*). Stripped bars on the right show the ratio of replicates in which no IGP was recorded. The asterisk indicates a significant asymmetry for the IGP interaction (Exact binomial test of goodness-of-fit, two-tailed, $P < 0.05$).

3.4. *Intraguild predation per developmental stage*

Mortality of *S. interruptus* caused by IGP or competition with *S. subvillosus* during immature developmental stages was higher at high EGprey densities, than at low EGprey densities. Mortality of *S. interruptus* at high EGprey densities predominantly occurred during the prepupa (15.0 %) and pupa (20.6 %) stages. However, low mortality rates were also observed between L2 and L4 (1.2–4.6 %) (Fig. 2**A**). At low EGprey densities, the highest mortality was observed at the pupa stage (4.7 %). However, some mortality was also observed at L1 and L2 stages. Mortality of *S. subvillosus* attributed to the interactions with *S. interruptus* during immature developmental stages, on the other hand, was highest at low EGprey densities. Mortality of *S. subvillosus* at high EGprey densities predominantly occurred during the pupa (9.6 %) and prepupa (28.8 %) stages. At low EGprey densities, *S. subvillosus* mortality predominantly occurred between L1 and L3 and was significantly high (40.5–52.9 %) (Fig. 2**B**).

3.5. *Developmental time*

Overall, developmental time from egg to adult was similar for the two predator species ($F = 2.87$; df = 2, 281; $P = 0.091$). EGprey density and EGprey diet influenced the predator developmental time (EGprey density: $F = 13.4$; df = 1, 281; $P = 0.0003$: EGprey diet: $F = 6.75$; df = 2, 281; $P = 0.0014$). Although a global intraguild interaction effect on developmental time was not observed (IGI: $F = 1.08$; df = 1, 281; $P = 0.299$), this is explained by the cross-over interactions. The effect of predator co-occurrence on the developmental time was different at the two distinct EGprey densities (IGI × EGprey density: $F = 16.24$; df = 1, 281; $P < 0.0001$). This influence changed depending on the predator species (IGI × EGprey density × species: $F = 6.12$; df = 2, 281; $P = 0.0025$) and the type of EGprey diet (IGI × EGprey density × species × EGprey diet: $F = 4.44$; df = 6, 281; $P = 0.0003$).

The developmental time of *S. subvillosus* was reduced in the presence of *S. interruptus* and at high EGprey densities of *A. spiraecola* and mixed diet. A reduction trend was also observed for the *A. gossypii* diet, although that was not significant (Table 3). Intraguild interaction effects on the developmental time of *S. interruptus* were nevertheless not so evident. No developmental time changes were observed under the *A. spiraecola* EGprey diet. On the other hand, this parameter was reduced at high EGprey densities of *A. gossypii*. Both high and low EGprey densities of the mixed diet increased *S. interruptus* developmental time.

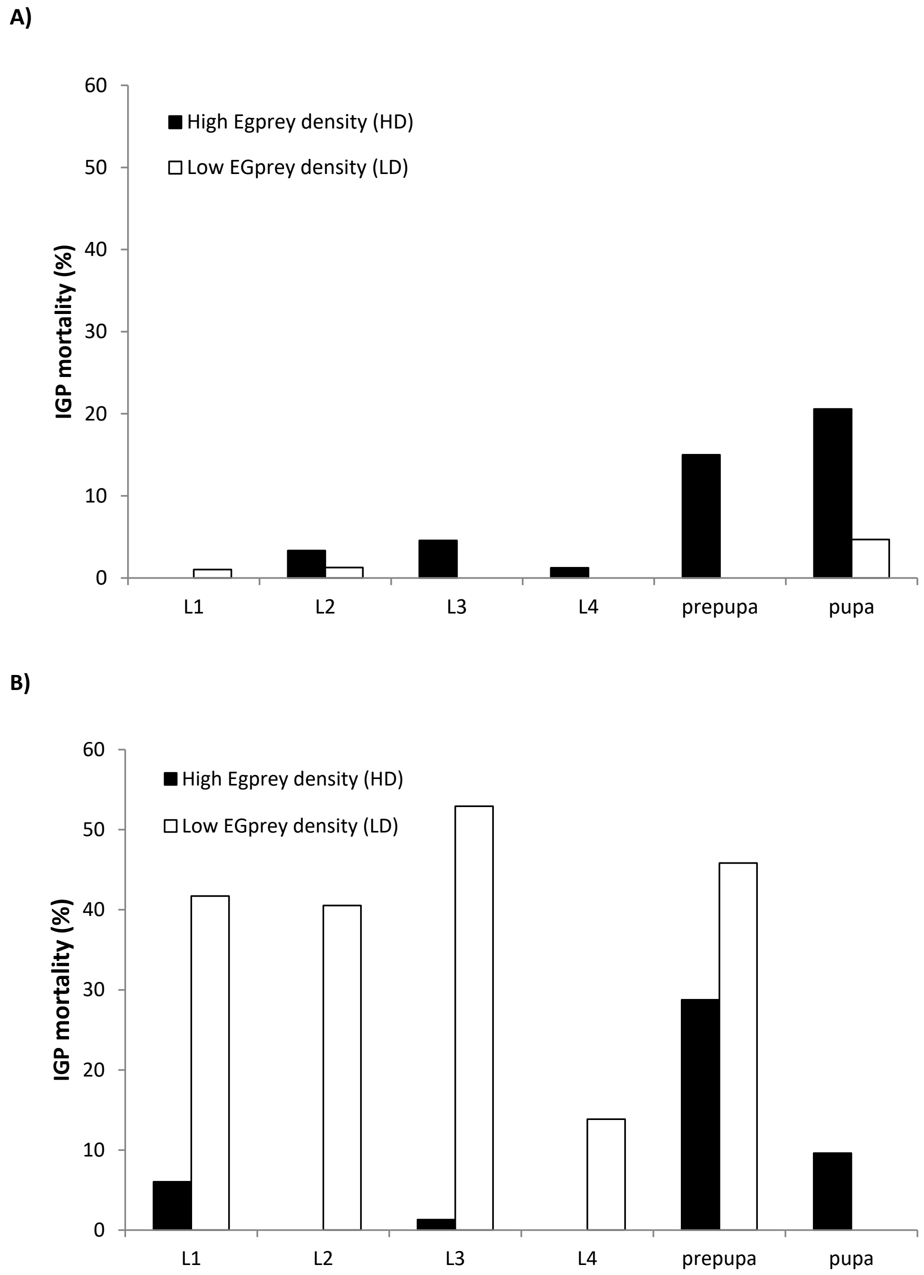

Fig. 2. Predator mortality attributed to IGP (%) in immature developmental stages (L1, L2, L3, L4, prepupa and pupa) of **A)** *S. interruptus* and **B)** *S. subvillosus* at high prey density (HD) and low prey density (LD).

3.6. *Adult size*

The intraguild interactions between the two predator species during their immature stages affected the emerging adults' size (IGI: $F = 38.48$; df = 1, 465; $P < 0.0001$). Intraguild interaction effects were similar for the two predator species (IGI × species: $F = 0.22$; df = 1, 460; $P = 0.6419$), for both males and females (IGI × gender: $F = 0.04$; df = 1, 460; $P = 0.833$) and the three diets (IGI × EGprey diet: $F = 0.69$; df = 2, 460; $P = -0.4997$). Adults of the two predator species under IGI and at high EGprey densities were significantly larger than those under IGI at low EGprey densities and those of the control treatment (Table 4). Although with marginal differences, the few surviving *S. subvillosus* adults under IGI at low EGprey densities were smaller than those of the control treatment ($t = 2.65$; df = 460; Adjusted $P = 0.088$).

4. Discussion

The present study reveals the complexity of scenarios in which the two predominant coccinellid species associated with *A. gossypii* and *A. spiraecola* in western Mediterranean citrus agroecosystems engage, and it unveils, by simulating those scenarios under laboratory conditions, the intricate intraguild interactions that unfold between them, including consumptive (IGP) and non-consumptive effects, when they share the same patch and food resource. The nature of these interactions underwent variations contingent upon factors such as the accessibility to their primary food resource (EGprey density) and quality (aphid species) which are constantly changing in citrus agroecosystems.

The coexistence of immatures from both *Scymnus* species, sharing the same aphid colony as a food resource, emerged as a relatively common occurrence during the spring major flushing period in our study. Encounters between the two species were observed across a diverse array

Table 3
Developmental time (mean ± SE) from egg-hatching to adult emergence of *S. interruptus* and *S. subvillosus* under intraguild interactions and in its absence, at high and low EGprey densities and with three types of EGprey diet (*A. spiraecola*, *A. gossypii*, and a mixed diet of both aphid species). The number of replications for each treatment combination it is displayed within the brackets. For each predator species, EGprey diet and EGprey density combination, significant differences in developmental time between predators under IGI and predators without IGI (control) are indicated with one asterisk ($P < 0.05$) (LS-means differences).

EGprey Diet	EGprey density/ IGI	Developmental time	
		S. interruptus	*S. subvillosus*
A. spiraecola	HD-IGI	17.36 ± 0.29 (33)	**15.56 ± 0.16*** (33)
	HD-control	17.38 ± 0.21 (15)	**16.54 ± 0.37*** (15)
	LD-IGI	18.32 ± 0.35 (26)	——— (26)
	LD-control	17.50 ± 0.22 (15)	16.25 ± 0.31 (15)
A. gossypii	HD-IGI	**15.38 ± 0.44*** (36)	14.88 ± 0.15 (36)
	HD-control	**16.93 ± 0.25*** (14)	15.45 ± 0.21 (15)
	LD-IGI	16.32 ± 0.46 (30)	——— (30)
	LD-control	17.63 ± 0.18 (13)	16.33 ± 0.49 (11)
Mixed diet	HD-IGI	**17.35 ± 0.33*** (22)	**15.80 ± 0.21*** (22)
	HD-control	**16.31 ± 0.17*** (13)	**18.08 ± 0.37*** (14)
	LD-IGI	**17.90 ± 0.18*** (25)	——— (25)
	LD-control	**16.44 ± 0.18*** (11)	——— (12)

Table 4
Adult size (area in mm^2 ± SE) of *S. interruptus* and *S. subvillosus* that were under IGI from L1 to adult emergence, at high and low EGprey densities, and adult size of the control predators (without IGI) fed at high EGprey densities during their preimaginal development. For each predator species, different letters indicate significant differences ($P < 0.05$; Tukey test).

	Adult size (mm^2)	
EGprey density/IGI	*S. interruptus*	*S. subvillosus*
HD-control	8.52 ± 0.11b	10.6 ± 0.12b
HD-IGI	9.73 ± 0.18a	11.6 ± 0.13a
LD-IGI	8.93 ± 0.17b	9.23 ± 0.73b

of scenarios, encompassing abundant food resource patches featuring already developed aphid colonies, as well as scenarios with limited food availability, such as already predated aphid colonies and incipient aphid colonies. The observed high frequency of encounters between larvae from both coccinellid species across this broad spectrum of scenarios suggests that species coexistence may be facilitated by complex intraguild interactions arising from this diversity.

Laboratory simulations suggested that IGP was bidirectional, but its dynamics varied strikingly in response to EGprey densities. At high EGprey densities, IGP between *S. interruptus* and *S. subvillosus* assumed a symmetric and relaxed form. Conversely, under conditions of scarce EGprey availability, a strong and asymmetric IGP emerged, characterized by *S. interruptus* frequently adopting the role of IGpredator and targeting *S. subvillosus* as IGprey. Unlimited availability of an essential prey seemed to deter the apex predator, *S. interruptus*, from attacking its competitor— a behavioural phenomenon previously documented in other coccinellid guilds preying upon aphids (Lucas et al., 1998; Kajita et al., 2000). Coupled with the previously observed higher ability of the EGprey (*S. subvillosus*) to exploit the essential prey (Bouvet et al., 2019b), this suggests that high aphid infestation in citrus orchards could foster the co-occurrence of the IGprey alongside its IGpredator. The co-occurrence of predators in IGP systems has traditionally been explained as a trade-off between their competition and their susceptibility to IGP (Holt and Polis, 1997). According to this theory, it is expected that the IGprey should be displaced in environments rich in food resources. This is because the capacity to exploit EGprey becomes less critical when food resources are not a limiting factor. This theoretical scenario was nevertheless not observed in this study and broader literature (Arim and Marquet, 2004). Instead, the diminished IGP activity of the apex predator appeared to contribute to a marginal increase in the IGP activity of the habitual intraguild prey, *S. subvillosus*. A recent study from Royer et al. (2024) postulates that more docile predators, in our case *S. subvillosus*, have the ability to exacerbate their aggressiveness with increasing EGprey availability. Remarkably, the least intense IGP manifested at high EGprey densities within a mixed diet of the two aphid species. The coexistence of *A. gossypii* and *A. spiraecola*, even sharing the same colony, is a frequent occurrence in citrus orchards within our study region, as shown in our field evaluations. The superior net reproductive rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ_m) observed for *S. subvillosus* when fed with mixed colonies of the two aphid species (Bouvet et al., 2019b) suggest that its prevalence thrives under high aphid infestations levels, especially within mixed prey colonies, where IGP upon it remains atypical. Conversely, the classical theory postulates that resource-scarce environments exclude the IGpredator, due to its weaker competitive capacity in exploiting the EGprey (Holt and Polis, 1997). Strikingly, in our study, the IGprey (*S. subvillosus*) experienced its highest mortality in these resource-poor scenarios. While the IGprey may be a better competitor for the EGprey, it appears insufficient to offset the intense IGP effects of the IGpredaotr (*S. interruptus*). Moreover, the observed high mortality rates of *S. subvillosus* at low EGprey densities, even in the absence of the IGpredator (51.4 %), suggest that the quantity of prey may be a more limiting factor for this species compared to *S. interruptus*. The competition between the two intraguild predators for a scarce food resource may exacerbate the effects of a low-resource diet. Field observations also show that *S. interruptus* usually increases its relative abundance concerning *S. subvillosus* during the citrus flushing periods of summer and fall when aphid infestations are much less abundant than those of spring (Bouvet et al., 2019a, c), thus supporting the theory that the strong and asymmetric IGP observed at low EGprey densities would favour a presence of the apex predator, *S. interruptus*.

Intraguild interactions constitute the synergistic interplay of two key behaviours: competition and IGP (Marques et al., 2018). The corrected mortality across distinct preimaginal developmental stages of both predators unveils dissimilar prevalence of these interaction mechanisms, differentiating between predators and in alignment with the availability of the EGprey. Irrespective of EGprey abundance, instances of *S. interruptus* mortality attributed to intraguild interactions were primarily concentrated during the pre-pupal and pupal stages. This observation suggests that *S. subvillosus* typically avoids direct predation on *S. interruptus*. However, interference competition between these predator species imposes certain fitness costs upon *S. interruptus* larvae, particularly when EGprey availability is not a constraining factor. These costs manifest predominantly as elevated mortality rates during the metamorphosis of *S. interruptus* into the adult stage.

The intraguild mechanisms driving mortality in *S. subvillosus* nevertheless appear to shift in response to EGprey availability. At high EGprey densities, mortality-inducing mechanisms in *S. subvillosus* mirror those observed for *S. interruptus*; mortality primarily manifests during the pre-pupa and pupa stages. This suggests that interference competition governs the intraguild dynamics between these two predator species in scenarios of abundant EGprey. In contrast, at low prey densities, the interaction between the predators is chiefly resolved with the death of *S. subvillosus* during these interactions (elevated rates of IGP-induced mortality during the active developmental stages, especially from L1 to L3). This pattern underscores the prominence of asymmetric IGP targeting *S. subvillosus* as the driving force in such scenarios.

In addition to the direct lethal effects of IGP and competition, the nonconsumptive effects (NCEs) stemming from intraguild interactions hold significant implications for the relationship between predators and, ultimately, for their biological control of the EGprey (Perdikis et al., 2014). The developmental time from egg hatching to adult emergence can serve as a gauge of predator fitness (Michaud, 2005) and wields a direct influence on population growth rates (Abrams et al., 1996). Mortality rates during preimaginal stages have previously exhibited correlations with the mean developmental times from egg to adult, as well as with adult size —although the latter is not anticipated to be unidirectional (Abrams et al., 1996). These two parameters provide valuable insights into sublethal effects resulting from the predators' intraguild interactions. Involved predators modified their juvenile developmental time; however, the magnitude of this modification varied distinctly for each predator species and was further contingent on the abundance and type of EGprey. The symmetric and weak IGP observed at high EGprey densities manifested as a reduced developmental time of the IGprey (*S. subvillosus*). Conversely, such a unidirectional effect was not observed for *S. interruptus*. It appears that the habitual IGprey may utilizes this shortened developmental time as a strategy to mitigate exposure to the IGpredator, although some fitness costs could be expected from this. Shorter developmental time could confer an advantage to the IGprey in scenarios simulating low IGP. High densities of *A. gossypii* emerged as the sole context in which *S. interruptus* displayed a reduction in its developmental time. This observation aligns with prior research indicating the predator's enhanced adaptation to *A. gossypii* diets (Bouvet et al., 2019b), suggesting that the shorter developmental times could provide an added competitive advantage to the IGpredator under high infestation levels of *A. gossypii*. The low survival rates of *S. subvillosus* immatures under IGP conditions and low EGprey densities prevent conclusions regarding the effects on its developmental time. Intraguild interactions between the two predators at low EGprey densities barely affected the developmental time of the habitual IGpredator (*S. interruptus*). The pronouncedly asymmetric nature of the described IGP relationships implies that *S. interruptus* need not alter its developmental time in the presence of the heterospecific competitor.

The adult size of coccinellids holds a direct correlation with their fitness, exerting influence over longevity, reproductive parameters, and resilience to environmental fluctuations (Michaud, 2005; Vargas et al., 2012). The impact of intraguild interactions on adult size displayed distinct nuances in terms of intensity and symmetry. The existence of a weak and symmetric IGP between the juveniles of the two predators led to an augmentation in their adult size. In the case of *S. subvillosus*, the habitual IGprey, no trade-off was observed in adult size despite the observed acceleration of its developmental time at high EGprey densities. Analogous outcomes were documented by Michaud et al. (2016) where an accelerated developmental time of coexisting specialist aphid predators did not entail a reduction in body size. This anomalous behaviour is hypothesized to arise from the evolutionary adaptation of aphidophagous coccinellids in resource-competitive environments (Michaud et al., 2016). The faster development of *S. subvillosus* without a cost on the adult body size may also explain why this species is usually dominant in high aphid infestations, despite its status as the IGprey. Strong and asymmetric IGP did not significantly affect adult size, but a trend to smaller sizes in the IGprey and bigger sizes in the IGpredator were observed. These findings are consistent with the results of this study, wherein low EGprey density scenarios favoured the IGpredator (*S. interruptus*) and impaired the IGprey (*S. subvillosus*).

In summary, the intraguild interactions, IGP and competition, between two sympatric and congeneric predator species, both associated with aphid infestations in citrus agroecosystems, exhibit a dynamic nature. The strength, symmetry, and underlying mechanisms of these interactions are subjected to fluctuation, primary driven by variables that continually shift within agroecosystems, such as the availability and quality of EGprey. While *S. interruptus* typically assumes the role of the IGpredator, our study has demonstrated instances of reciprocal IGP. The dynamic interplay may offer valuable insights into the coexistence of the two prominent aphid predators in western Mediterranean citrus agroecosystems. Specifically, the coexistence of the two *Scymnus* species appears to hinge on weak and symmetric IGP, often associated with the heightened aphid infestations characteristic of the spring citrus flushing period. This condition not only facilitates their co-occurrence but also tilts the balance in favour of *S. subvillosus*, which boasts superior life-history parameters and a seemingly well-adapted competitive edge for shared resources. Conversely, during the summer and fall citrus flushing periods, marked by low EGprey densities, strong and asymmetric IGI would favour *S. interruptus*. Temporal changes in IGI between these predators prompt a temporal niche partitioning, with a relative dominance of the IGprey in spring and the IGpredator prevailing in summer and fall. It is worth noting that other unexplored mechanisms, such as the ability of these predators to exploit alternative food sources and the influence of habitat structure, may further contribute to their coexistence (Janssen et al., 2007; Calabuig et al., 2018; Bouvet et al., 2019c). A deeper understanding of the trophic relationships between these two predators, essential preys in citrus, and essential and alternative preys associated with other plant species in the agroecosystem, will be a valuable tool for the development of more effective conservation biological control strategies involving these coccinellid species.

CRediT authorship contribution statement

J.P.R. Bouvet: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. **A. Urbaneja:** Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Supervision, Writing – original draft, Writing – review & editing. **C. Monzo:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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.

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During the preparation of this work the author(s) used ChatGPT openai in orderTo review grammar inaccuracies of the final draft of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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