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RESEARCH ARTICLE

Birds and bats differ in pest control pathways in fruit orchards: Intraguild and direct predation

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Abstract

1. Birds and bats are relevant natural enemies of pests in fruit crops. However, by preying also on arthropod natural enemies, they may act as intraguild predators that can lead to pest release. Disentangling how these two groups intervene in different ecological relationships is thus essential to understand their relative contribution and complementarity in pest control provision.
2. We used dietary DNA metabarcoding to build tri-trophic networks that account for direct and indirect interactions among top predators (birds and bats), mesopredators (spiders) and pests (insects) in apple and blueberry crops. To identify species closely linked to pests, we estimated modularity. To evaluate their topological and tri-trophic role, we quantified their centrality and the extent of distinct predatory pathways in their diets (i.e. direct pest predation, intraguild predation or both). Finally, in the case of birds in apple crop, we tested if the topological and tri-trophic role of species depended on their abundance, degree of insectivory and morphological traits.
3. The network was modular in both crops, with birds and bats occupying distinct modules feeding on different prey. Bats tended to be more directly connected to pests than birds, which were more frequently involved in intraguild predation. Among birds in the apple crop, higher abundance increased direct pest predation, whereas greater insectivory favoured intraguild predation. Morphology further shaped topological position, with smaller species with less pointed wings demonstrating higher centrality values.
4. Birds and bats showed different and complementary roles in pest control service, a pattern consistent among fruit crops. Both vertebrate groups were associated

with different prey, and birds were more prone to promote pest release than bats, although such effect was weaker for common and less insectivorous species.

5. *Synthesis and applications*. Our study highlights that by combining interaction networks, tri-trophic cascades and species traits, we can better understand the role of species on the control of pests in fruit crops. In particular, our results point out that promoting bats and abundant birds may be an efficient strategy to enhance pest control in fruit orchards.

KEYWORDS
agroecosystems, apple and blueberry crops, centrality, interaction motifs, intraguild predation, modularity, northern Spain, pest control

1 | INTRODUCTION

Birds and bats are effective agents of pest control in agroecosystems (Monteagudo et al., 2023; Tuneu-Corral et al., 2023), consuming different types of pests and with distinct daily and seasonal patterns (Chaves et al., 2026; Maas et al., 2016). This complementary foraging broadens pest control to include a wider range of pests and their potential outbreaks (Garfinkel & Johnson, 2015; Snyder, 2019). Nonetheless, both groups also feed on arthropod natural enemies (Schmitt et al., 2021; Vansynghel et al., 2022), engaging in intraguild predation interactions that can counteract or even outweigh their positive effects on pest suppression (Martin et al., 2013; Pejchar et al., 2018). Consequently, their net effect on pest control can only be assessed by considering both the complementarity between these groups and the role of intraguild predation. Selective exclusion experiments have evidenced differential relative contributions of birds and bats to pest control (e.g. Maas et al., 2016; Vansynghel et al., 2022). However, these approaches do not make it possible to identify the key interactions that link birds and bats with pests, which are often influenced or altered by mesopredators such as spiders.

Such complexity can be tackled through the use of metabarcoding, to identify prey spectra in predators' diets, and translate this information into interaction networks (Chaves et al., 2026; Mata et al., 2021; Ollivier et al., 2021). The network approach allows to analyse how birds and bats are linked with pests, while considering intraguild predation (Delmas et al., 2019). In this sense, network modularity describes the tendency of species (nodes) to form subgroups (modules) that interact more frequently (Newman, 2006), indicating functional complementarity and specialization when, for example, different predators consume different sets of prey species (Allen et al., 2022; Blüthgen & Klein, 2011). Beyond the global network structure, measuring the relative contribution of species to network topology (i.e. the overall structure of the network; how species are arranged and connected through their interactions) also help to interpret the role of single species for interaction dynamics and their derived ecological functions (Delmas et al., 2019). Species centrality within the network represents their ability to account for a large proportion of interactions while interconnecting different trophic levels or ecological functions (e.g. García et al., 2024). Moreover, interaction networks can accommodate information across trophic levels to infer the role of species in trophic cascades (Delmas et al., 2019). This role can be assessed by subdividing networks into motifs, which are recurrent patterns of interactions among small sets of nodes in different positions (Meyer et al., 2020; Milo et al., 2002). Combining centrality with trophic motifs seems necessary to fully understand the functional relevance of species in trophic networks. Importantly, by analysing the effects of species abundance and traits on their network roles we can distinguish the impact of different mechanisms (neutral vs. deterministic) underpinning species contributions to pest control (García et al., 2024; Laigle et al., 2018; McLeod et al., 2020).

Here, we applied a DNA metabarcoding-informed network approach to evaluate the contribution of birds and bats to pest control in fruit crops. We considered a tri-trophic perspective of pest control accounting for direct and intraguild predation, by incorporating spiders, a major arthropod group feeding on crop pests (Mezőfi et al., 2020), but also being preyed upon by birds and bats (Andriollo et al., 2021; Gunnarsson, 2007). We focused on co-occurring apple and blueberry crops in northern Spain. We hypothesized that birds and bats would provide complementary, but mechanistically distinct, pest control pathways, with patterns consistent across crops. Based on previous research in the region about bird and bat assemblages composition in the fruit orchards (Martínez-Sastre et al., 2020; Miñarro & García, 2025) and their diet (Jiménez-Albarral et al., 2025; Miñarro et al., 2026), we predicted that: (1) Networks would be modular, with birds and bats tending to segregate into different modules reflecting dietary partitioning; (2) bats would be more strongly associated with direct pest predation, whereas birds would show greater involvement in intraguild predation via spiders and thus would be topologically more central; and (3) variation in network roles among bird taxa would be influenced by abundance and traits, with more abundant, insectivorous and canopy-dwelling species occupying more central positions and showing higher intraguild predation. To test these predictions, we quantified modularity, centrality and motif profiles in crop-specific tri-trophic networks in apple and

blueberry orchards, and related bird roles to abundance and traits in apple orchards. Replication across co-occurring crop systems and their associated pests within the region allowed us to assess the consistency of the observed network patterns.

2 | MATERIALS AND METHODS

2.1 | Study system

The study was conducted in the region of Asturias, in northern Spain (Appendix S1, Figure S1.1), an area with temperate oceanic climate with high, evenly distributed rainfall. Apple (*Malus* × *domestica*) stands as the preeminent fruit crop in Asturias, with most plantations dedicated to cider production and based on local cultivars (Dapena et al., 2005). Among arthropod pests, the most important are codling moth (*Cydia pomonella*), aphids (*Dysaphis plantaginea*, *Aphis* spp. and *Eriosoma lanigerum*) and apple blossom weevil (*Anthonomus pomorum*) (Miñarro et al., 2011). Blueberry is a relatively recent and minor crop in the region, but rapidly expanding, and orchards are typically planted with two or more cultivars belonging *Vaccinium corymbosum* and *V. ashei*. Currently, there is no evidence of heavy pest damage by arthropods in Asturian orchards, except from the invasive spotted-wing drosophila (*Drosophila suzukii*). Fruit production in Asturias remains low intensity, with small-sized orchards of both crops normally co-occurring and embedded within heterogeneous landscapes comprising pastures, crops, eucalyptus plantations and natural woody vegetation, including hedgerows, forests and shrublands (Figure S1.1). This environment favours highly diverse communities of arthropods (Hambäck et al., 2021; Miñarro et al., 2011), birds (Jiménez-Albarral et al., 2025; Martínez-Sastre et al., 2020) and bats (Miñarro & García, 2025) in orchards.

2.2 | Field procedures

To construct comprehensive tri-trophic networks for apple and blueberry crops, we merged data from multiple sources (orchard, sites, years) containing information on the occurrence and the ecological interactions of birds, bats and arthropods. Sampling was conducted in orchards representative of local management practices and regional landscape features. Since datasets span multiple years and differ in spatial scope (Figure S1.2), our inference assumed a degree of environmental stability (e.g. due to climate, regional land use, management regimes) sufficient to preserve the core of dominant interactions across years and sites for the purposes of this study. We therefore interpreted the resulting tri-trophic networks as spatially and temporally aggregated, integrative networks for each crop. These networks describe interaction potential between birds, bats and arthropods in the study region rather than interactions within specific orchard communities. For a comprehensive description of field procedures, see Appendix S1.

2.2.1 | Bird sampling

We quantified bird assemblages in three apple and three blueberry orchards (Figure S1.3) using repeated point counts (apple: August 2019 to July 2020; blueberry: May to September 2022). We identified species and counted all individuals heard or seen in a 50-m radius from the sampling location and estimated relative abundance as the cumulative number of individuals recorded per crop. We captured birds using mist nets in the same orchards (apple: August 2019 to July 2020; blueberry: May to September 2022 and 2023) to collect fresh faecal samples and measure morphological traits.

2.2.2 | Bat sampling

We quantified bat activity in 20 apple orchards and three blueberry orchards using passive acoustic detectors during four night-sessions from spring to autumn 2022 (Figure S1.3). We used the total duration of bat calls recorded per orchard-night as a proxy of relative bat abundance by crop type (see Miñarro & García, 2025). For diet metabarcoding, we collected bat faecal samples from 17 roosts within ≤1 km of apple or blueberry orchards (Figure S1.1), visiting roosts approximately every 2 weeks from spring 2022 to autumn 2023, and storing samples at −20°C until DNA extraction. Bat species identity was confirmed using DNA barcoding techniques (see Appendix S1 for more details). We collected samples from 5 of 12 potential bat species or species complexes recorded foraging in the study orchards (Miñarro & García, 2025).

2.2.3 | Spider sampling

In June 2016, we sampled spiders in 10 apple orchards using a standardized beating method on apple trees (Figure S1.3). In blueberry crop, individuals were collected directly from plants in three blueberry orchards on four occasions between May and September 2022 in three orchards (Figure S1.3). All specimens were stored at −20°C until DNA extraction. Spiders were identified visually to the most resolved taxonomic level, and relative abundances were calculated by pooling individuals across orchards within each crop type.

2.3 | Molecular and bioinformatic procedures

We selected a subset of faecal samples for molecular analysis, ensuring that different species, sites (i.e. orchards and roosts), and dates were represented. Samples were processed in four batches, due to logistical constraints, with minor protocol modifications between batches to optimized DNA extraction and amplification. Here, we summarize the most relevant among batches (see Appendix S1 for a detailed description of all procedures).

We analysed 546 samples from 26 bird species from apple orchards, 282 samples from 11 bird species from blueberry orchards, 375 samples from 5 bat species from roosts nearby apple and blueberry orchards, 210 samples from 48 spider species from apple orchards, and 467 samples from 58 spider species from blueberry orchards. Bird and bat DNA was extracted using a silica solid-phase protocol (Longmire et al., 1997; Rohland & Hofreiter, 2007), whereas spider DNA was extracted using QIAamp Micro Kit and DNeasy Blood & Tissue Kit (Qiagen, www.qiagen.com). We used different primer pairs to amplify regions of the mitochondrial cytochrome c oxidase (COI), and hence, they slightly differed between vertebrates and spiders. Invertebrate sequences from bird samples from apple orchards were clustered at a similarity threshold of 98% into operational taxonomic units (OTUs; Shutt et al., 2020) and identified with a 90% similarity threshold in the Robeson et al. (2021) database. For the remaining samples, sequences were used to infer amplicon sequence variants (ASVs) using the core sample inference algorithm (Callahan et al., 2016). For bats, birds and spiders captured in blueberry orchards, we employed a pre-trained classifier of the COInr reference database (Meglécz, 2022; version 2023-05-03) with additional polishing by AllGenetics and Biology SL (www.allgenetics.eu), with a 90% similarity threshold. For spiders from apple orchards, we used a 97% similarity threshold in the Barcode of Life Database (www.boldsystems.org; Ratnasingham & Hebert, 2013).

2.4 | Statistical analyses

2.4.1 | Tri-trophic networks

We applied a network approach in which vertebrate, spider and pest taxa were nodes (Delmas et al., 2019) and interactions between taxon pairs were links indicative of energy flow or regulatory potential between prey and predators (Cirtwill et al., 2018). First, for each predator group and crop (i.e. birds, bats and spiders), we constructed a predator–prey matrix with data from metabarcoding analyses focussing on prey taxa defined as apple or blueberry pests, that is, phytophagous species feeding on apple trees or blueberry plants according to literature and online resources. For birds and bats, we also incorporated spider taxa consumed as prey into the interaction matrix. Since our focus was on comparing the direct and indirect links between vertebrates and pests through spider mesopredators, we did not consider predatory interactions among spiders, treating them simply as an intermediate trophic level. Moreover, spider intraguild predation pathways were relatively uncommon among the spider taxa consumed by birds and bats (Figure S1.4), suggesting that their exclusion is unlikely to affect the patterns regarding tri-trophic roles of birds and bats.

From the original predator–prey interaction pool, we built five bipartite matrices for each crop (i.e. bird–spider, bird–pest, bat–spider, bat–pest and spider–pest). In each matrix, links between predator taxa and their prey were calculated as the weighted frequency of occurrence (wPOO) of the prey in the diet. The percentage of occurrence (POO) measures the representation of each prey taxon in the diet of each predator (Deagle et al., 2019) and was weighted by the relative abundance and the degree of insectivory of the predator taxon. In this way, we obtained a more realistic representation of energy flow within the community, since links of abundant or efficient predators contribute more strongly to the network structure (Cirtwill et al., 2018). Degree of insectivory was estimated as the proportion of invertebrates present in the diet relative to other food resources (fixed at 1 for bats and spiders as strict insectivores; variable for birds and obtained from the Elton Traits Dataset; Wilman et al., 2014). We modified the lowest value of degree of insectivory (0 out of 1 in the Elton Traits Dataset, but 0.1 out of 1 in the present case) because all bird species recorded were known to prey on arthropods in our assemblage (García et al., 2024).

We checked for interaction sampling completeness in the bipartite matrices through rarefaction analyses based on Hill numbers estimated with the *iNEXT* function of the *iNEXT* package (Hsieh et al., 2016) in R 4.3.0 (R Core Team, 2023). Sample coverage curves were based on incidence-frequency data derived from a random set of samples analysed for each predatory group. The values obtained were above or close to 50% sample coverage (Figure S1.5). While these values represent moderate completeness, we considered that they included the main core of interactions that are relevant for pest control. Therefore, we could merge, for each crop, the five bipartite matrices into a tri-trophic one that connects top predators (birds and bats) with mesopredators (spiders) and pests. Before merging matrices, we normalized all interactions by dividing them by the total sum, so that the sum of interactions of each bipartite network equalled 1 (Quintero et al., 2022). Additionally, not all taxa had the same taxonomic resolution in all datasets. When a taxon was identified at the species level within a matrix but only at the genus level in another matrix, the information was consolidated into the genus level in both networks. We employed the functions *matrix_to_list_bipartite* and *create_monolayer_network* in the R package *emln* (Frydman et al., 2023), to obtain the edge lists of the bipartite matrices and to merge them into the tri-trophic networks. To visualize the tri-trophic networks, we used the software Gephi 0.9.7 applying the Yifan Hu algorithm (Bastian et al., 2009).

2.4.2 | Network modularity

To search for network modules, we derived a quantitative value of global network modularity using the *Infomap* algorithm in the *infomapecology* R package (Farage et al., 2021) over 1000 iterations. To evaluate whether the modularity value significantly departed from random expectations, we used the null model vaznull from the *bipartite* package (Dormann et al., 2007). For each bipartite matrix, we generated 1000 randomized matrices in which the probability of interactions depended on taxa abundance and merged them in null tri-trophic networks. Modularity was calculated for each merged null network, and the significance of the empirical modularity value was assessed using *t*-tests.

2.4.3 | Topological and tri-trophic roles of bird and bat species

We quantified the topological relevance of bird and bat species in the tri-trophic network per crop with centrality metrics, reflecting the influence from a given node (taxa) on the rest of the network. We employed three centrality metrics: degree, harmonic closeness and undirected betweenness (Cirtwill et al., 2018; Delmas et al., 2019). Degree measures the number of links or interactions of each node, which corresponds to the diet generality of predators within the context of trophic interactions (Jordán et al., 2006). Harmonic closeness measures how close a taxon is to all others via shortest paths, considering forbidden interactions between taxa pairs (e.g. between birds and bats). It reflects the efficiency of a taxon to influence the overall network. Finally, undirected betweenness describes the number of paths passing through a taxon, both directly and indirectly, indicating the potential of that taxon to connect modules or trophic levels. Together, closeness (proximity) and betweenness (intermediation) provide complementary dimensions of the role of top predators in network connectivity through tri-trophic interactions (Delmas et al., 2019). Closeness and betweenness were computed on edge costs defined as the inverse of interaction strength (1/weight), so that stronger interactions correspond to shorter paths (Costa et al., 2019). Analyses were performed with the function's *degree*, *harmonic_centrality* and *betweenness* included in the *igraph* R package (Csárdi et al., 2006). We employed generalized linear models (GLMs), using the R-base function *glm*, to compare the values of centrality metrics between bats and birds. We used a negative binomial for degree (log link), a gamma for closeness (log link) and a hurdle gamma model for betweenness.

To estimate the tri-trophic role of birds and bats in the network of each crop, we identified three trophic motifs from predators to pests: (i) direct pest predation, (ii) intraguild predation and (iii) trade-off loops (Figure 1; Cirtwill et al., 2018). Direct pest predation refers to predation events where a vertebrate or a spider feed on a pest. Intraguild predation occurs when a vertebrate preys on a spider that consumes a pest. Trade-off loops are a particular case of intraguild predation, where a vertebrate consumes both the predatory spider and, separately, the pest. For each bird and bat taxon, we calculated the proportion of each motif (i.e. i, ii and iii) and compared these proportions between groups using a beta regression (using *betareg* R package, Cribari-Neto & Zeileis, 2010). In addition, we conducted a correlation stratified by predator group between centrality metrics and the proportion of each motif to evaluate if the topological position of birds and bats indicate their tri-trophic role. Stratified correlation was estimated through a gaussian regression, with robust estimation to account for non-normality. Response and explanatory variables were scaled (mean = 0, and SD = 1) and vertebrate group was used as a random effect. For this analysis, we used the function *rlmer* in the R package *robustlmm* (Koller, 2016).

2.4.4 | Ecological determinants of the topological and tri-trophic role of species

To understand the impact of abundance and traits on the role of top predators, we focused exclusively on birds captured in apple orchards, the only group with a sufficiently high number of species to conduct regression analysis ($N = 25$). As features, we considered degree of insectivory and morphological traits. To summarize morphological traits, we used their projection on a principal coordinates analysis (PCoA) based on species body weight (g), beak length (mm), gape width (mm), Kipp's index (a measure of wing pointiness, estimated from Kipp's distance divided by wing length), tarsus length and tail length (mm). For all traits, we used species averages obtained during mist netting. The first PCoA axis was positively related with beak and body size, while the second axis represented a gradient towards a higher Kipp's index and a shorter tarsus (see Jiménez-Albarral et al., 2025). Relative abundance, degree of insectivory, their interaction and the two PCoA axes were used as predictors of regression models with the different measures of centrality and proportion of motifs as response variables. The models for closeness and betweenness included only PCoA axes, as the calculation of these response variables accounted for the relative abundance and degree of insectivory for edge weights. For network centrality measures, we fitted generalized linear models (GLMs) using *glm*, specifying a negative binomial distribution for degree (log link), a gamma distribution for

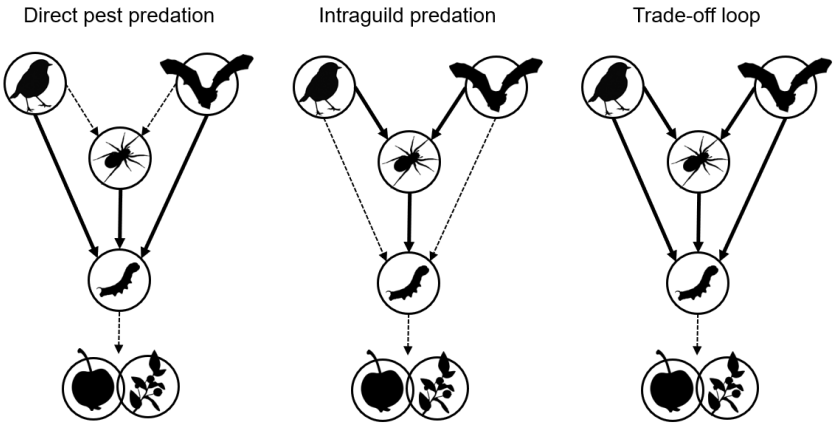

FIGURE 1 Trophic motifs based in the tri-trophic interactions between vertebrates (bats and birds), spiders and pests in fruit orchards. Continuous arrows depict the combination of interactions characterizing each motif. Silhouettes sourced from PhyloPic.

closeness (log link) and a hurdle gamma model for betweenness. For the proportion of motifs, we applied beta regression models (logit link) using the *betareg* function from the *betareg* package in R (Cribari-Neto & Zeileis, 2010).

2.5 | Permits and ethics

The Government of the Principality of Asturias provided the necessary permits for scientific ringing (2019/014907, AUTO/2020/581). Bird capture followed ethical guidelines and minimized disturbance.

3 | RESULTS

3.1 | Tri-trophic networks

The tri-trophic network in apple orchards contained 25 bird, 5 bat, 39 spider, and 91 pest taxa, and 623 interaction events. Birds accounted for 67% of interactions, bats for 23% and spiders (as predators) for 9%. Interactions were unevenly distributed across species with two bat species (*Pipistrellus pipistrellus* and *Rhinolophus hipposideros*) and two bird species (*Parus major* and *Sylvia atricapilla*) accounting for 36% of all interactions involving top predators. These percentages should be interpreted as descriptive summaries of the assembled networks, as they may also be influenced by differences in the number of samples analysed of each taxon and predator group. The network showed a clear core-periphery structure, with most pests in peripheral positions and connected to a core of generalist predators, whereas some specialist predators remained sparsely connected in the periphery (Figure 2a). Most bird species were found in the central core, alongside spiders. In contrast, bats were slightly displaced and mainly connected to peripheral pests. We found similar patterns in the tri-trophic network in blueberry orchards (Figure 2b). This network comprised 10 birds, 5 bat, 42 spider, and 46 pest taxa, and 300 interaction events. Birds accounted for 55% of the total interactions, bats for 34% and spiders for 11%, with the same four vertebrate species dominating the interactions of top predators.

3.2 | Network modularity

The Infomap algorithm detected 16 and 12 modules in the apple and blueberry networks, respectively (Figure S1.6). These degrees of

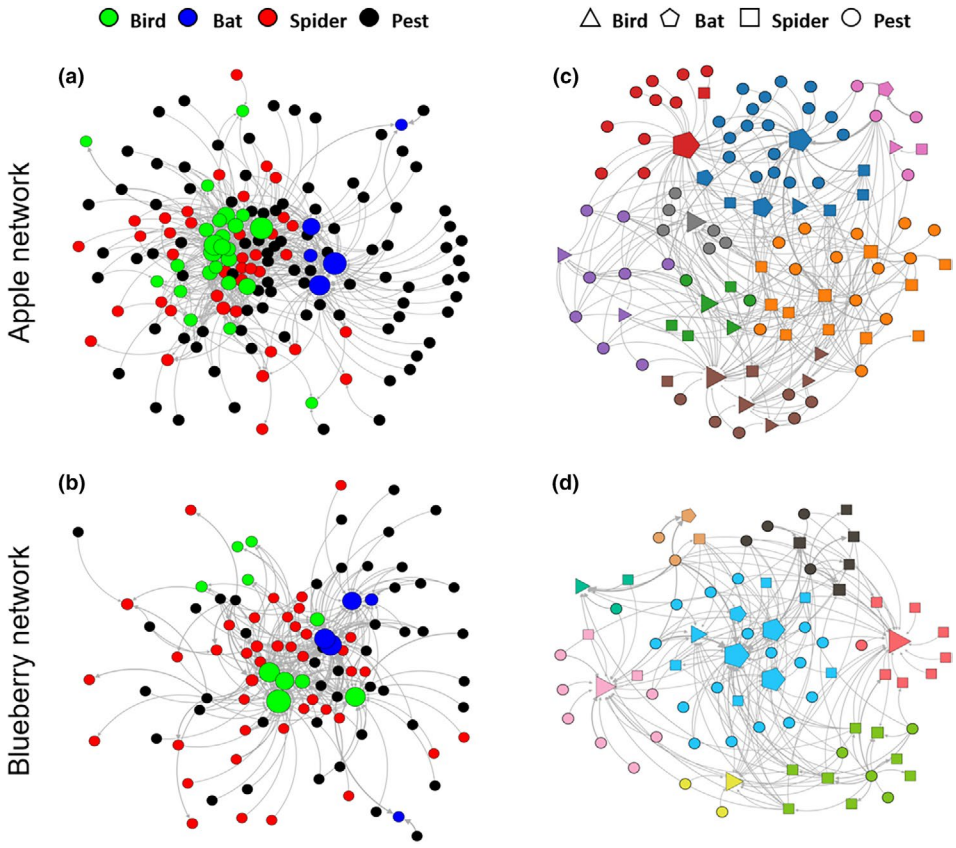

FIGURE 2 Structure of the tri-trophic interaction network in apple and blueberry orchards. (a, b) Nodes represent taxa, with colours indicating the group (i.e. birds, bats, spiders and pests), links represent interactions. Size of nodes is scaled with taxon's in-degree. (c, d) Subnetwork containing the eight largest modules (comprising 58% and 74% of all taxa in apple and blueberry network, respectively). The nodes have been placed ad hoc to emphasize module display. The colours of nodes (taxa) indicate the module, shapes the group (i.e. birds, bats, spiders and pests).

modularity were higher than anticipated by random processes based on taxa abundances (Figure S1.7). Eight large modules encompassed 58% of the interacting taxa in the apple network and 74% in the blueberry network (Figure 2c,d; Figure S1.6). Birds and bats were often in different modules, and they only coexisted in two of them in the apple network and in one in the blueberry network (Figure 2c,d). In addition, some modules comprised a single predator group coupled to pests, for example, a bird–pest module or a spider–pest module, indicating that distinct consumer types aggregate different sets of pests within modules. Although bats did not constitute the sole predatory group in any module, they dominated some with few birds and/or spiders present (Figure 2c,d).

3.3 | Topological and tri-trophic roles of bird and bat species

Centrality metrics were positively correlated within crops (Spearman's correlations rho ≥ 0.43, $p \leq 0.02$, in all cases except degree–closeness correlation in blueberry network, rho = 0.36, $p = 0.19$). In the apple network, degree did not vary between birds and bats ($\beta = -0.52$, $p = 0.15$), whereas closeness was markedly lower in birds ($\beta = -1.62$, $p < 0.01$). For betweenness, the probability of having non-zero values did not vary ($\beta = -1.05$, $p = 0.38$) but, among species with positive betweenness, birds showed substantially lower values than bats ($\beta = -1.66$, $p = 0.02$). In the blueberry network, centrality metrics did not reveal differences between bird and bat species (degree $\beta = -0.36$; $p = 0.37$; harmonic closeness $\beta = 0.03$; $p = 0.97$; undirected betweenness positive part $\beta = -0.96$; $p = 0.24$) (Figure 3a–c).

In total, we detected 705 motifs involving trophic interactions from top predators to pests in the apple network, and 168 in the blueberry one. Among these, intraguild predation was the most represented in both crops (51 and 54% of motifs in apple and blueberry orchards), followed by direct pest predation (31 and 32%), while trade-off loops were scarcely represented (11 and 14%, respectively) (Figure 3d–f). In both crops, direct pest predation was the most common motif for bats (61 and 70% of them in apple and blueberry networks). Also, bats showed higher values of direct pest predation than birds, a difference supported by the beta regressions (apple: $\beta = -1.09$; $p = 0.03$; blueberry: $\beta = -2.16$; $p < 0.01$). Meanwhile, intraguild predation was the most frequent motif in birds, accounting on average for 56% and 41% of birds' motifs (apple network and blueberry network, respectively). Nonetheless, the beta regressions did not indicate differences between birds and bats in the proportion of intraguild predation (apple: $\beta = 0.89$; $p = 0.07$; blueberry: $\beta = 0.80$, $p = 0.20$) or trade-off loops (apple: $\beta = 0.38$; $p = 0.37$; blueberry: $\beta = 0.16$, $p = 0.71$). This was probably because of the high variability among bird species. In general, the centrality of top predators was a poor indicator of the importance of distinct interaction motifs in which they were involved. We only found a positive correlation between the proportion of trade-off loops and centrality metrics (apple: degree $\beta = 0.71$, $p < 0.01$; blueberry: degree $\beta = 0.87$, $p < 0.01$; closeness $\beta = 0.48$, $p = 0.01$; betweenness $\beta = 0.54$, $p = 0.01$).

3.4 | Ecological determinants of topological and tri-trophic roles of bird species

Generalized linear models (GLMs) showed that, in the apple network, birds' degree increased with abundance but decreased with body size (PCoA axis 1) and Kipp's index (PCoA axis 2) (Table 1; Figure 4a–c). Closeness was negatively associated with Kipp's

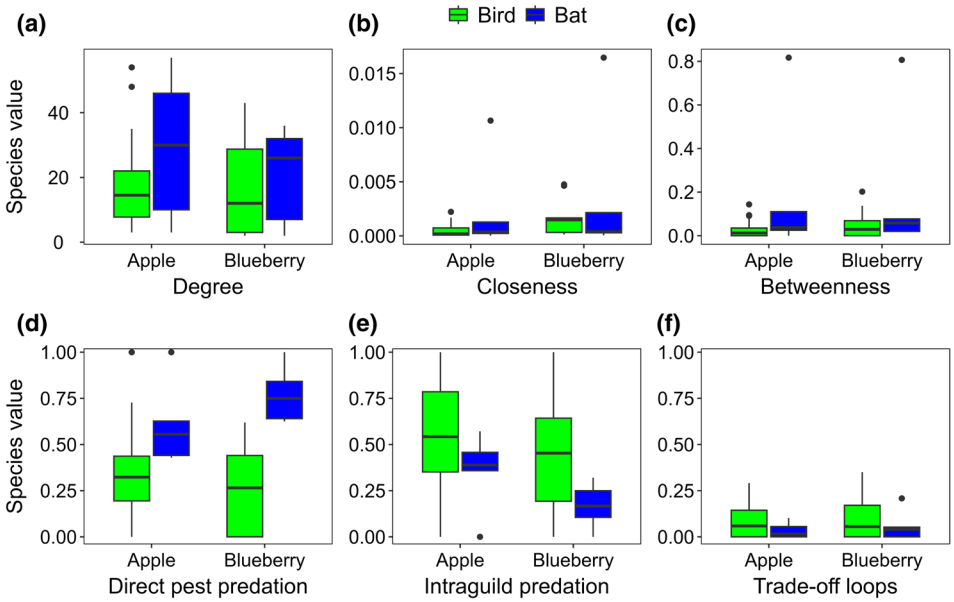

FIGURE 3 (a–c) Centrality metrics for bird ($N = 25$) and bat ($N = 5$) species within the tri-trophic networks of different crops. (d–f) Proportion of interaction motifs for bird and bat within the tri-trophic networks.

TABLE 1 Results of generalized linear models (GLMs) and beta regressions evaluating the effects of bird species' relative abundance, insectivory and morphological traits (i.e. PCoA axis 1 and 2), on centrality metrics and the proportion of motifs in the apple network.

	Estimate	SE	z/t	p
Degree—Negative binomial (log); $R^2=0.668$				
(Intercept)	2.65	0.10	26.97	<0.01
Relative abundance	**0.46**	**0.11**	**4.40**	**<0.01**
Insectivory	0.07	0.10	0.69	0.49
PCoA axis 1	**−0.34**	**0.11**	**−3.21**	**<0.01**
PCoA axis 2	**−0.28**	**0.13**	**−2.22**	**0.04**
Relative abundance|Insectivory	−0.07	0.17	−0.42	0.674
Closeness—Gamma (log); $R^2=0.22$				
(Intercept)	−7.81	0.22	−36.17	<0.01
PCoA axis 1	−0.04	0.22	−0.18	0.86
PCoA axis 2	**−0.62**	**0.22**	**−2.82**	**0.01**
Betweenness—Hurdle-logit part: Binomial (logit)				
(Intercept)	0.40	0.44	0.89	0.37
PCoA axis 1	0.63	0.52	1.20	0.23
PCoA axis 2	−0.28	0.50	−0.57	0.57
Betweenness—Hurdle-positive part: Gamma (log); $R^2=0.06$				
(Intercept)	−3.39	0.23	−14.75	<0.01
PCoA axis 1	**−0.56**	**0.19**	**−2.91**	**0.01**
PCoA axis 2	**−1.09**	**0.19**	**−5.83**	**<0.01**
Direct pest predation—Beta (log); $R^2=0.45$				
(Intercept)	−0.84	0.18	−4.73	<0.01
Relative abundance	**0.50**	**0.19**	**2.59**	**0.01**
Degree of insectivory	**−0.48**	**0.18**	**−2.61**	**<0.01**
PCoA axis 1	0.00	0.16	0.01	0.10
PCoA axis 2	0.12	0.18	0.64	0.53
Relative abundance|Degree of insectivory	**−1.09**	**0.30**	**−3.68**	**<0.01**
Intraguild predation—Beta (log); $R^2=0.46$				
(Intercept)	0.47	0.17	2.76	<0.01
Relative abundance	**−0.62**	**0.19**	**−3.22**	**0.01**
Degree of insectivory	**0.42**	**0.18**	**2.31**	**0.02**
PCoA axis 1	0.08	0.16	0.51	0.61
PCoA axis 2	−0.04	0.18	−0.23	0.82
Relative abundance|Degree of insectivory	**0.99**	**0.30**	**3.35**	**<0.01**
Trade-off loops—Beta (log); $R^2=0.31$				
(Intercept)	−2.18	0.18	−12.49	<0.01
Relative abundance	**0.35**	**0.18**	**2.00**	**0.05**
Degree of insectivory	0.11	0.16	0.68	0.50
PCoA axis 1	−0.23	0.16	−1.44	0.15
PCoA axis 2	−0.12	0.19	−0.63	0.53
Relative abundance|Degree of insectivory	0.10	0.28	0.34	0.73

Note: Significant effects ($p<0.05$) are shown in bold.

index (PCoA axis 2) (Table 1; Figure 4d), and betweenness with both morphological variables (Table 1; Figure 4e,f). Beta regressions revealed that bird abundance and degree of insectivory strongly influenced the occurrence of interaction motifs (Table 1; Figure 4g–k). Abundant and less insectivorous species were more involved in direct pest predation, while rare and highly insectivorous species showed higher frequencies of intraguild predation. Trade-off loops were mainly associated with abundance. Morphological traits did not affect the proportion of motifs (Figure S1.8).

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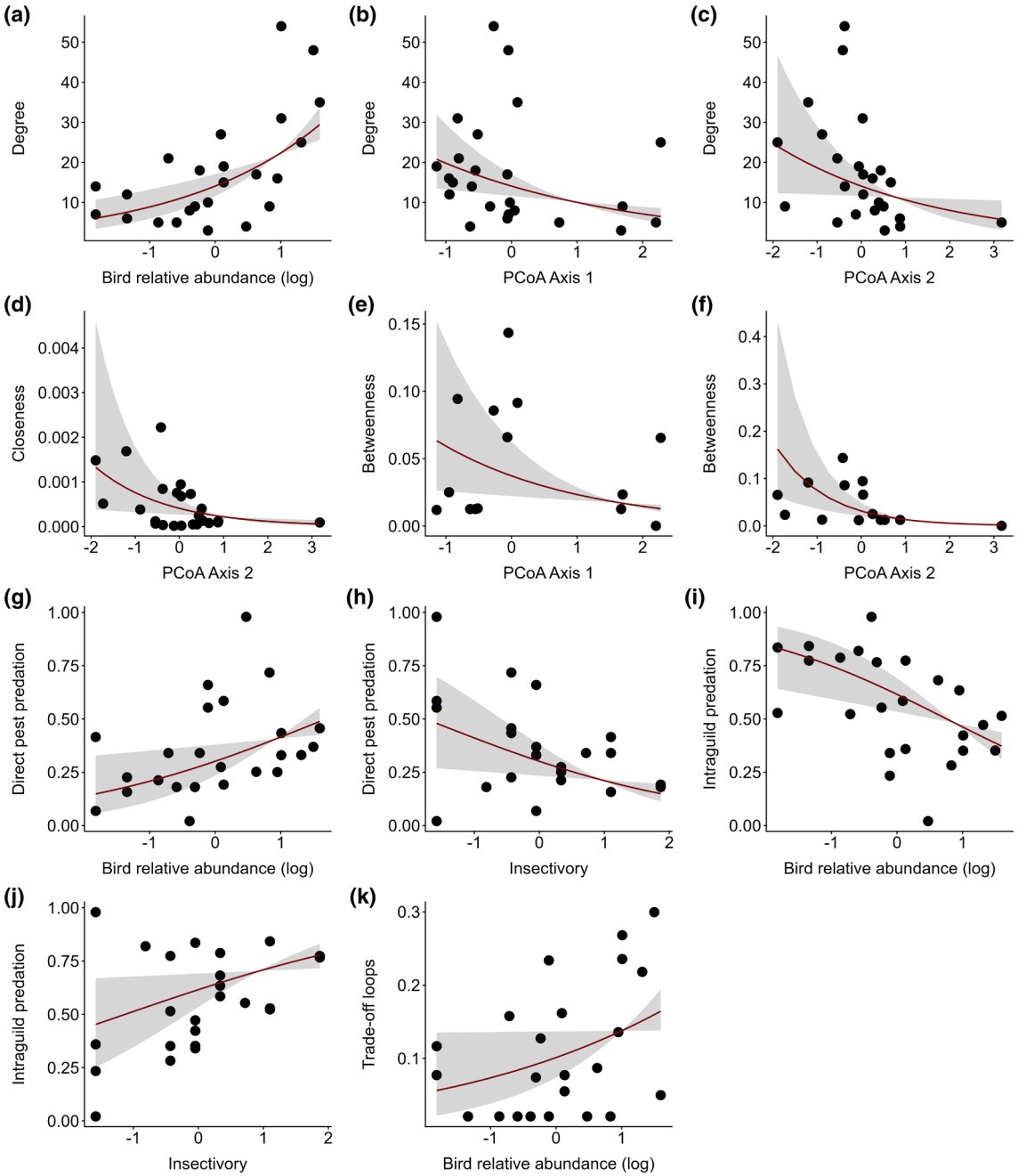

FIGURE 4 Significant relationships between bird relative abundance, insectivory and morphology (PCoA axes), and centrality metrics (a–f) or the proportion of interaction motifs (g–k) in the apple network. Points represent bird species; red lines indicate mean model predictions and shaded areas show 95% confidence intervals.

4 | DISCUSSION

In this study, we constructed tri-trophic networks linking birds and bats with spiders and pest arthropods to infer their respective ecological roles in Asturian apple and blueberry orchards. Our approach revealed complex interactions between top predators, mesopredators and basal prey. Birds and bats often occupied different modules and interacted preferentially with different prey taxa. In addition, their position as predators within networks indicated contrasting contributions to pest regulation. Birds, particularly those rare and highly insectivorous species, tended to occupy positions closer to spiders, reflecting greater involvement in intraguild predation cascades. In contrast, bats were separated from the bird–spider cluster and more often connected to pests through direct predation. Taken together, these findings indicate dietary complementarity between birds and bats, but not necessarily an equivalent role in pest control within orchard-based agroecosystems. The similarity in network structure and the topological and tri-trophic roles of vertebrates across crops suggests generalized assembly patterns associated with pest control by birds and bats in fruit crop systems of the region.

4.1 | Network modularity

As expected in antagonistic interactions, the studied tri-trophic networks exhibited a high degree of modularity (Newman, 2006), with interaction clustering being higher than that expected from a random encounter of taxa (see also Suzuki et al., 2023). These findings are consistent with those reported for bipartite bird/bat–pest networks (García et al., 2024; Mata et al., 2021). Moreover, they reinforce the idea of functional complementarity between these two groups of top predators which show spatio-temporal segregation (Maas et al., 2016), and due to their foraging behaviour and phenology, they often target different developmental stages of the same taxa (e.g. leaf-dwelling caterpillars vs. flying adults; Karp & Daily, 2014). In addition, in our study area, birds and bats present distinct habitat preferences, with birds more frequently associated with higher cover of semi-natural forest (García et al., 2018) and bats more commonly present in rural urbanized areas (Miñarro & García, 2025). Here, we demonstrate that this complementarity extends to their dietary preferences impacting the entire network of interactions.

4.2 | Network roles of birds and bats

Birds and bats also occupied distinct positions within the networks, with important implications for their potential role in pest control. Topology metrics revealed no differences in degree between birds and bats in any crop, indicating a comparable number of prey items per species across groups. By contrast, in apple orchards, closeness and betweenness were higher in bats, indicating that they occupy intermediate positions within the tri-trophic web (Cirtwill et al., 2018; Delmas et al., 2019). These differences disappeared when the most common bat species, *P. pipistrellus*, was excluded from the analyses. Common Pipistrelle showed disproportionately high values of centrality because it was highly connected in general, and in particular to spiders (e.g. *Theridion* spp. and *Clubiona* spp.) and pests (e.g. *Pandemis heparana* and *C. pomonella*) with central positions (Guimerà & Amaral, 2005). In the case of blueberry, *P. pipistrellus* also exhibited the highest closeness and betweenness values, but these were not sufficient to elicit significant differences between the groups. The disproportionate role of *P. pipistrellus* in network centrality agrees with its dominance within bat assemblages in the studied agroecosystem (Miñarro & García, 2025).

The motif-based approach evidenced that birds and bats differed in their tri-trophic roles. Importantly, these motif comparisons were conducted considering spiders as a single intermediate trophic level. Although intraguild predation by spiders occurred in the study system (see Hambäck et al., 2021), including such links would have generated longer trophic pathways and nested intraguild predation loops (e.g. vertebrate–spider–spider–pest) that fall beyond the scope of the present study. Bats were more involved in direct pest predation than birds, and hence, may be more effective natural enemies. This finding contrasts with previous exclusion experiments in tropical crops, which evidenced frequent intraguild spider predation by bats and in a higher frequency than birds (Karp & Daily, 2014; Maas et al., 2013). Differences with previous work may reflect the foraging behaviour of birds and bats in our study area. Birds usually glean prey from foliage (Morrison et al., 2018), whereas bats tend to prey in flight (Dietz & Kiefer, 2016). Thus, birds may encounter spiders more frequently, pointing out that they, on average, may be less efficient in pest control. Notably, this idea contrasts with the generally positive effects of pest predatory birds on plants and crops reported by global syntheses (Boesing et al., 2017; Díaz-Siefer et al., 2022; Mäntylä et al., 2011; Philpott et al., 2009), a pattern also evidenced in Asturian apple orchards (García et al., 2018). This may respond to the fact that although birds were more involved in intraguild predation, they preyed upon all most important pests of the studied crops (*C. pomonella*, *D. plantaginea*, *Aphis* spp., *E. lanigerum*, *A. pomorum*, *D. suzukii*), especially the most common species (*P. major*, *S. atricapilla*, *Erithacus rubecula rubecula*). Bats, in turn, only preyed on *C. pomonella* and *D. suzukii*. Therefore, some important pests may be only controlled by birds.

Our simultaneous analysis of species centrality and interaction motifs suggested that the position of birds and bats within networks did not directly reflect their tri-trophic role. Although bats tended to occupy more central positions in the network, which could suggest a greater involvement in intraguild predation, a closer examination of their interactions revealed that they primarily acted as direct predators of pests rather than as intraguild predators mediated by spiders. Therefore, to infer the actual role of top predators, we need to consider both types of metrics. Topological centrality will inform about the influence in general energy fluxes, whereas motifs will refine this information from the point of view of pest control. It is important to note that the imbalance in the number of species of the different vertebrate groups within the networks increases the influence of dominant taxa, particularly *P. pipistrellus*, on group-level patterns. Such influence may be especially relevant for absolute network metrics such as degree, which should be interpreted as a relative measure of trophic generalism rather than as a precise estimate of interaction richness. Nevertheless, this is unlikely to represent a major source of bias, as *P. pipistrellus* is the most abundant and widespread bat species associated with fruit orchards in the region (Miñarro et al., 2026; Miñarro & García, 2025).

4.3 | Ecological determinants of topological and tri-trophic roles of bird species

Abundance and morphology affected bird topological role within networks, with abundant, smaller-bodied species and with less pointed wings consuming a higher number of prey species and occupying more central positions. These trait combinations plausibly enhance manoeuvrability and foraging performance within tree canopies (Carrascal et al., 1990; Gleditsch & Sperry, 2020), thereby increasing encounter rates with key phytophagous prey (e.g. Lepidoptera larvae, aphids) and with their spider predators. In contrast, avian tri-trophic role was more related to their degree of insectivory.

Abundant and less insectivorous birds tend to show higher direct predation rates. The higher rates of direct pest consumption exhibited by commoner species seems related to a probabilistic effect: Random encounter frequency with pest taxa is expected to increase in the more abundant species (Peralta et al., 2020). These abundance effects may even compensate for the lower impact of highly insectivorous species in terms of direct pest predation, ultimately determining a significant top-down control of pests exerted by the whole bird assemblage in apple orchards (García et al., 2018; Jiménez-Albarral et al., 2025). In other words, direct vertebrate impacts on pests can outweigh any weakening of mesopredator control via intraguild predation (Mooney et al., 2010). Furthermore, in our system, very abundant but less insectivorous bird species, such as *E. rubecula* and *S. atricapilla* (which account for 15% and 14% of relative abundances), were more frequently involved in trade-off loops. In these motifs, intraguild links co-occur with direct predation on the same pest sets, partially offsetting expected disservices and buffering pest release (Mitchell & Neutel, 2012; Simmons et al., 2019). Therefore, abundant generalists not only consume more pests via direct predation, but they are also less likely to trigger intraguild-mediated pest release.

4.4 | Study limitations

Here, we combined metabarcoding-inferred interactions among birds, bats, spiders and pests to map tri-trophic pathways of pest control in apple and blueberry orchards. While this approach captures species level interactions in detail, some limitations remain. Although metabarcoding enables the detection of trophic interactions that are otherwise difficult to observe, estimates of interaction strength may be affected by primer choice and bioinformatic pipeline biases. Differences in bioinformatic pipelines across datasets may affect taxonomic resolution, potentially influencing the identification of some interactions (Brandt et al., 2021; Mathon et al., 2021). However, overall ecological patterns appear to be poorly affected by such methodological differences (dos Santos & Blabolil, 2025). Importantly, birds and bats were sequenced using the same primer pair, thereby controlling for primer bias across the focal groups (Forsman et al., 2022), but this was not possible in spiders, for which more taxon-specific primers were required. Thus, to improve quantitative comparability among predator groups, we prioritized incidence over read counts, harmonized taxonomy across matrices and applied grand total standardization before merging the bipartite matrices (Callahan et al., 2017; Glassman & Martiny, 2018; Quintero et al., 2022). Therefore, we consider our approach to be among the most robust currently available for integrating interaction data across distinct predator taxa.

Another potential problem with using DNA metabarcoding is that it may detect spurious interactions via secondary predation (i.e. DNA from the gut contents of prey consumed by the focal predator; Deagle et al., 2019). This inflates the proportion of trade-off loops that actually reflect intraguild predation. Since secondary prey DNA is expected to occur in lower quantities and in a more degraded state, filtering out reads representing less than 0.1% relative abundance (see Appendix S1) likely minimized this issue. Although the application of empirical thresholds derived from experimental controls has been demonstrated to increase precision (Drake et al., 2022), such approaches are often difficult to implement in highly diverse food-web studies, such as the present one. The fixed threshold employed here represents a pragmatic compromise between retaining true interactions and reducing artefacts arising from contamination, sequencing errors or secondary predation. The effects of different filtering thresholds are comparatively small when results are averaged across many individuals (Cirtwill & Hambäck, 2021). However, such treatment could potentially overlook actual rare links and low-frequency prey items, which may already be under-detected due to the moderate sampling coverage suggested by rarefaction analyses (Chiu et al., 2023; Jordano, 2016). In principle, the underrepresentation of rare interactions can affect network topology and the estimates of species role (de Aguiar et al., 2019; Llopis-Belenguer et al., 2023). Nevertheless, because our network metrics were weighted by interaction frequency, rare interactions are unlikely to substantially alter the main patterns observed. Moreover, ecosystem services such as pest control are primarily driven by frequent interactions (Kremen, 2005), and hence, focusing on the network core provides an appropriate framework for evaluating the potential roles and complementarity of predators. Having said so, our network should be used with caution when interpreting the role of species beyond the core of common interactions.

Our tri-trophic networks were assembled by merging interaction datasets collected across different spatial and temporal scales. Although this is a common approach, and we followed established procedures such as grand-total standardization (Quintero et al., 2022), combining interaction datasets inherently assumes a certain degree of temporal stability in community composition and interaction structure throughout the sampling period. While this assumption may not hold at the level of individual orchards, it is reasonable for aggregates, regional-scale networks such as the examined here. Of particular concern are the spider–pest interactions in apple orchards, given that they emerged from a sampling restricted to June. Such narrow temporal coverage may underestimate these interactions and affect the inferred importance of intraguild predation. To assess the robustness of our results to such temporal mismatches between datasets, we conducted an additional sensitivity analysis restricted to samples from apple orchards collected in June, ensuring temporal overlap among trophic levels (see Appendix S2). This analysis yielded qualitatively consistent results, which, together with the similar outcomes observed across crops, indicates that the main network patterns observed are temporally robust. Between 2016 and 2023, mean temperatures increased and rainfall slightly decreased, consistent with regional climatic trends. However, the frequency of extreme events (e.g. days with maximum temperatures exceeding 35°C or 40°C), which are most likely to alter trophic interactions, remained unchanged (Taboada et al., 2025). Furthermore, we detected no major changes in land use or orchard management over this period. The proportion of the main habitats (i.e. forests,

pastures, wood plantations and apple orchards) remained stable between 2015 and 2025 (Martínez-Sastre et al., 2020; Morán-López et al., under review). Taken together, despite the limitations of metabarcoding and multi-source network integration, our approach provides a consistent framework for identifying the main trophic pathways underpinning pest control in these fruit crop systems.

5 | CONCLUSIONS

The complementary roles of bats and birds in pest control have been observed in several studies (Bouarakia et al., 2023; Chaves et al., 2026; Karp & Daily, 2014; Maas et al., 2013, 2016; Vansynghel et al., 2022). Our study adds a new dimension of complementarity, highlighting how these vertebrates interact with distinct pests, and hence, the presence of both groups may favour more comprehensive pest control. Even though birds would be, in principle, less effective due to intraguild predation, abundant species interacted with a high number of pests and did so more directly. Therefore, they may favour pest control in a wide array of major pests. Overall, these results highlight that it is imperative to ensure the optimal conditions for the core of dominant predators, which in turn sustains pest control (Gaston et al., 2018; Winfree et al., 2015). Management measures can support this goal (Lindell et al., 2018), although this can be challenging for favouring birds and bats due to their distinct habitat preferences. At the landscape level, given that the specific preferences of both groups differ (more birds with higher forest cover, more bats near urbanized rural areas; García et al., 2018; Miñarro & García, 2025), the most effective course of action would be to maintain heterogeneous, fine-grained mosaics that enhance more diverse assemblages of both birds and bats, and foster their spatial co-occurrence. At the orchard level, effective management of hedgerows has been shown to be beneficial for both groups, as it provides food resources, refuge and connectivity (Montgomery & Reid, 2025). For birds, the installation of nest boxes has been proved a highly effective measure in the study system (García et al., 2021). While we lack evidence for the suitability of artificial bat roosts in the Asturian region, this measure, in conjunction with the promotion and conservation of water sources and other foraging habitats, is generally suggested (Tuneu-Corral et al., 2023). Together, these practices can help leverage the complementary roles of birds and bats to maintain multi-trophic pest control in agroecosystems. These management actions may be easily promoted if added to the schedules of public subsidies for biodiversity-friendly farming, as it is the case of apple orchards in Asturias where a bird-oriented programme is currently ongoing (BOPA, 2025).

AUTHOR CONTRIBUTIONS

Daniel García, Teresa Morán-López, Marcos Miñarro and José Javier Jiménez-Albarral conceived the ideas; José Javier Jiménez-Albarral, Teresa Morán-López, Agustín Vitali, Juan Carlos Illera, Marcos Miñarro, Peter A. Hambäck and Daniel García designed methodology; José Javier Jiménez-Albarral, Daniel García, Marcos Miñarro and Peter A. Hambäck collected and curated the data; José Javier Jiménez-Albarral, Teresa Morán-López and Agustín Vitali analysed the data; José Javier Jiménez-Albarral led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests or personal relationships that could have appeared to influence the work reported in this paper. Daniel García is an Associate Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data and code supporting the results of this study are available from the Zenodo repository at https://doi.org/10.5281/zenodo.18692181 (Jiménez-Albarral, 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Details on field and laboratory procedures and complementary results.

Figure S1.1. (A) Schematic representation of study area, depicting the region of study (Asturias province in dark grey within the

peninsular Spain), and the location of the apple orchards, blueberry orchards and bat roosts where data were collected. (B) Aerial view of an apple orchard (in red) and a blueberry orchard (in blue) in the study area. (C) Photograph of an apple orchard ©Marcos Miñarro. (D) Photograph of a blueberry orchard ©Manuel Soto.

Figure S1.2. Workflow of data integration and network construction. Bird, bat and spider datasets differed in sampling period, spatial coverage and data source. For each predator group, diet metabarcoding data were used to construct predator–prey interaction matrices. The resulting bipartite matrices were taxonomically harmonised and standardised before being merged into crop-specific tri-trophic networks. These networks were subsequently used to quantify modularity, species centrality and tri-trophic motifs.

Figure S1.3. Schematic representation of study area, depicting location of the apple and blueberry orchards where data were collected. Bird sampling consisted in bird censuses and mist-netting to collect fresh faecal samples. Bat sampling consisted in bat censuses with acoustic detectors (AudioMoth, Open Acoustic Devices). Spider sampling consisted in the collection of individual specimens.

Figure S1.4. Distribution of the proportion of intraguild predation (IGP) among bird, bat and spider taxa in the apple tri-trophic network. The histograms show species frequencies, with rug marks indicating individual observations. Red dashed lines represent median values.

Figure S1.5. Rarefaction curves of predator-prey interactions richness and sample coverage, per sampling effort unit (number of samples of predatory species analysed), for different interaction types. Symbols represent the observed values and the dashed line the extrapolated values expected with higher sampling effort. (A) and (B) show data from apple orchards; (C) and (D) show data from blueberry orchards.

Figure S1.6. Representation of the tri-trophic networks observed in (A) apple orchards and (B) blueberry orchards between vertebrates (birds in green and bats in blue), spiders (in red) and pests (in black). Actual interactions between species pairs are shown in coloured squares. Each colour represents interactions between species pairs belonging to the same module, and the grey squares represent those between species pairs belonging to different modules.

Figure S1.7. Histograms with the frequency of the number of modules of 1000 randomized networks originated by the Vaznull null-model in (A) apple orchards and (B) blueberry orchards. Red dashed line represents the number of modules in the observed tri-trophic network.

Figure S1.8. Non-significant relationships between bird insectivory and morphology (PCoA axes), and centrality metrics (A, B) or the proportion of interaction motifs (C–I) in the apple network. Points represent bird species.

Appendix S2. Sensitivity analysis of the apple tri-trophic network using temporally matched samples (June subset).

Figure S2.1. Structure of the apple tri-trophic network from the subset of June samples. (A) Nodes represent taxa, with colours indicating the group (i.e., birds, bats, spiders, and pests), links represent interactions. Size of nodes is scaled with taxon's in-degree. (B) Subnetwork containing the eight largest modules (comprising 82% of all taxa). The nodes have been placed ad hoc to emphasize module display. The colours of nodes (taxa) indicate the module, shapes the group (i.e., birds, bats, spiders, and pests).

Figure S2.2. Rarefaction curves of predator-prey interactions richness and sample coverage, per sampling effort unit (number of samples of predatory species analysed), for different interaction types. Symbols represent the observed values and the dashed line the extrapolated values expected with higher sampling effort.

Figure S2.3. Histogram with the frequency of the number of modules of 1000 randomized networks originated by the Vaznull null-model. Red dashed line despites the number of modules in the observed tritrophic network.

Figure S2.4. Representation of the apple tritrophic network from the subset of June samples between vertebrates (birds in green and bats in blue), spiders (in red) and pests (in black). Actual interactions between taxon pairs are shown in coloured squares. Each colour represents interactions between taxon pairs belonging to the same module, and the grey squares represent those between taxon pairs belonging to different modules.

Figure S2.5. (A–C) Values of centrality metrics for bird and bat taxa within the tri-trophic network. (D–F) Proportion of interaction motifs for bird and bat within the tri-trophic network.

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