



Common birds combine pest control and seed dispersal in apple orchards through a hybrid interaction network

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ABSTRACT

Farmland ecosystem services frequently result from different ecological functions simultaneous provided by specific biodiversity groups such as birds. These bundles of ecosystem services may be approached from inter-specific interaction networks, which inform about the structure of interactions while identifying the species more relevant for combining ecosystem services. Here, we studied how birds provide pest control in apple orchards, and seed dispersal in orchard-adjacent hedgerows and forests. For this, we used field data and DNA-metabarcoding of bird fecal samples, obtained across a whole year from three orchards in northern Spain, to build interaction networks between birds and arthropod apple pests, and between birds and non-crop fleshy-fruited plants. We addressed the structure of the different networks underpinning pest control and seed dispersal. We also combined both ecosystem services through a hybrid network to assess, by means of centrality measures, the topological roles of individual bird species and their ecological determinants. Interaction networks differed in structure, with pest-control network showing higher modularity and specialization than seed-dispersal network, otherwise characterized by high nestedness. These differences emerged from the different typologies, i.e. antagonistic vs. mutualistic, of the bird-pest and bird-plant interactions. The hybrid network integrating pest control and seed dispersal evidenced strong variability across birds in their role to connect ecosystem services, depending on their central or peripheral positions. Bird centrality was positively related with species abundance and independent of body size or diet diversity. This finding suggests the relevance of neutral processes (i.e. the random encounters of organisms) for driving inter-specific interactions, and it highlights the relevance of common birds for sustaining ecosystem service bundles in agroecosystems. The preservation of fruit-rich hedgerows and forest patches around apple orchards is an action recommended to maintain the populations of common bird species, responsible of both agricultural pest control and the natural regeneration of these habitats.

1. Introduction

Biodiversity is considered a pivotal feature of agroecosystems due to the provision of ecosystem services that render benefits in the form of crop production and/or stability (Power, 2010; Dainese et al. 2019). Many of these ecosystem services depend not only on species diversity *per se*, but on the complex array of trophic interactions among wild and crop species (Sheenan, 2008). For example, crop pest control is shaped

by the antagonistic interactions between different species of natural enemies and crop pests (e.g. Macfadyen et al., 2009), whereas crop pollination depends on the mutualism between pollinator animals and crop and adjacent wild plants (e.g. Allasino et al., 2023). To deal with and better understand this sort of biological complexity in agroecosystems, network approaches, where species are represented as nodes and ecological interactions are considered as connections (or links) between nodes, have been highly favored (Bohan et al., 2013;

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Allen et al., 2022).

Ecological networks inform on the global structure and function of interaction assemblages (Delmas et al., 2019). In this sense, structural differences between networks are expected to emerge from different interaction types (Fontaine et al., 2011). For example, antagonistic networks (e.g. predator-prey) tend to be highly modular (i.e. having clusters of interactions well differentiated within the network), whereas mutualistic networks (e.g. plant-pollinator) are usually lowly specialized (i.e. bearing few specialist species) but highly nested (i.e. containing supergeneralist species that monopolize interactions with both generalist and specialist partners; Fontaine et al., 2011). These structural divergences may encompass functional differences, as modularity and specialization may promote complementarity in the provision of ecosystem services, while generalization is a source of functional redundancy (Blüthgen and Klein, 2011; Allen et al., 2022). Identifying global structural patterns may be thus relevant for managing ecosystem services emerging from different types of networks co-occurring in the same agroecosystems (Pocock et al., 2012; Allen et al., 2022).

Another advantage of network approach is the potential to assess the differential contribution of individual species for maintaining the structure and the function of the whole network. This may be addressed through centrality, a measure of the topological position of a given species which depends on how many other species are linked to it, both directly and through intermediate species (Delmas et al., 2019). In this sense, a central species is highly connected to many different, distant parts of a network, whereas a peripheral species only connects a reduced and nearby part of the network (Delmas et al., 2019). Distinguishing central and peripheral species is critical when networks combine, through shared species, different types of interactions (i.e. hybrid networks, *sensu* Morrison et al., 2020) and, hence, simultaneously support different ecosystem services. For example, flower-strip plants used in many crops interact with flower-visitors that provide pollination and, at the same time, interrelate with parasitoids providing pest control (Windsor et al., 2021). Therefore, identifying the role of species in hybrid networks, as well as understanding their ecological determinants, is needed for managing synergies and trade-offs of ecosystem service bundles (Allen et al., 2022; Timóteo et al., 2023).

Birds represent a diverse group providing various trophic-based ecosystem services in agroecosystems (Whelan et al., 2008). For example, insectivorous birds exert biological control on arthropod pests in a variety of agroecosystems across different latitudes (Boesing et al., 2017; Díaz-Sieffer et al., 2022). Moreover, many birds depend on seminatural habitat patches embedding crops, such as hedgerows and forests, whose woody plants rely reciprocally on birds for seed dissemination and natural regeneration (Rey et al., 2021; González-Varo et al., 2021). Thus, by preying on arthropods and disseminating seeds, birds would be locally linking pest control and seed dispersal (Timóteo et al., 2023). Despite the relevance of this dual role of bird assemblages in agroecosystems, no study has yet explicitly evaluated the combination of these avian-mediated ecosystem services, or the ecological features of the species involved.

Here, we used DNA-metabarcoding of bird fecal samples to identify interactions between birds and arthropod crop pests, and between birds and non-crop fleshy-fruited plants in cider apple orchards of northern Spain. Then, we applied a network approach to understand the structure of pest control and seed dispersal services. In this agroecosystem, birds have been found to exert significant biological control (García et al., 2018, 2021) as well as to drive population dynamics of woody plants (Martínez and García, 2017; González-Varo et al., 2021). Specifically, we seek: 1) to compare the structure of interaction networks leading to the different services of pest control and seed dispersal; 2) to estimate the topological role (centrality) of bird species in a global, hybrid network considering both ecosystem services; 3) to address whether bird relative abundance, traits, and diet explain bird centrality. Ultimately, we interpret our findings in terms of management of animal-derived ecosystem service bundles.

2. Methods

2.1. Study system and study sites

The study was conducted in the cider apple (*Malus x domestica* Borkh.) croplands of central Asturias (N Spain; Fig. S1A). In this region, cider is a valuable traditional product, strongly ingrained in society, and linked to gastronomy and tourism. Most cider apple orchards are comprised of local cultivars, with a typical density of ca. 500 trees/ha, and with trees reaching frequently more than 5 m high. Orchards are relatively small (normally 0.5–4 ha). They are embedded in a highly variegated landscape (Fig. S1B) combining pastures, annual crops, other fruit orchards, timber plantations, human infrastructures, and seminatural woody vegetation such as hedgerows, temperate broad-leaved forests and heathland patches.

Apple orchards are typically surrounded, either totally or partially, by woody hedgerows and/or small forest patches which are mostly unmanaged by farmers (Fig. S1B-C; García et al., 2018). These small forests and hedgerows are rich in wild fleshy-fruited plants including trees (e.g. *Laurus nobilis*), treelets (e.g. *Cornus sanguinea*), shrubs (e.g. *Rubus fruticosus*) and vines (e.g. *Smilax aspera*; González-Varo et al., 2021).

Previous studies have found up to 53 species of wild birds inhabiting Asturian cider apple orchards, from which more than a half were considered as insectivorous and tree-dwelling species (García et al., 2018). The bird assemblage also harbors species being described as legitimate seed dispersers (i.e. dropping intact seeds of fleshy-fruited plants after regurgitation or defecation) of fleshy-fruited plants species (González-Varo et al., 2021).

At least 15 arthropod species have been recognized as agronomically relevant pests for cider apple crops in the Asturias region (Miñarro et al., 2011). These include fruit-seed predators (e.g. *Cydia pomonella*), sap-feeding aphids (e.g. *Dysaphis plantaginea*), and flower-ovule predators (e.g. *Anthonomus pomorum*). Other damaging phytophagous arthropods are leaf-feeder caterpillars (e.g. *Pandemis heparana*), leaf-miners (e.g. *Phyllonorycter blancardella*), leaf-eater weevils (e.g. *Polydrusus formosus*), sap-feeding small cicadas (e.g. *Cicadella viridis*), and leaf-roller cecidomyids (e.g. *Dasyneura mali*).

The study was carried out in 2019–2020 in three apple orchards located in the Villaviciosa municipality (43° 28' 44" N, 5° 26' 54" W), Asturias. Orchards were 0.8–5.3 ha size, separated from 1.5 to 4.55 km one from each other, and embedded in a *bocage*-type landscape with ca. 22% cover of seminatural-woody habitats comprising small forests, isolated trees, hedgerows and shrubland patches (Fig. S1B). All orchard showed woody hedgerows or adjacent forest in more than 60% of its perimeter, and apple production was based on a low-input agronomic scheme.

2.2. Mist-netting sampling

Bird mist-netting sessions were carried out every two weeks in each orchard, from August 2019 to July 2020. For each session, two mist nets were placed inside the apple plantation and three nets were placed at orchard borders, 2 m away from woody hedgerows (Fig. S1C). Mist-nets (16 and 19 mm mesh size) ranged between 9–18 m length and 2.5–3 m height (total capture area of 178.5 m²). They were installed just before dawn and removed around noon, remaining open for five consecutive hours and checked for bird captures every 45–60 minutes. Birds were kept up to 30–40 min inside clean ringing cloth bags to obtain defecations or regurgitations. All captured birds were marked with a unique numbered aluminum ring and individual measures of body weight, wing length, tarsus length, and gape width were taken. Each regurgitation or fecal sample found in the cloth bags was collected with a sterile swap and stored in the field at 4°C until final storage at –20°C in laboratory. We placed a 1 m-wide plastic mesh band of 1 mm pore below each mist net to easily locate on the ground any seed expelled by birds while

trapped in the nets, which would be otherwise hardly detected if dropped into the grassy ground of the orchards (Rumeu et al., 2023). Seeds located on the mesh when checking for bird capture were collected for further identification and assigned to the specific bird trapped in the vertical.

2.3. Bird censuses

For bird censuses, we established a sampling station within each apple orchard, 25 m away from orchard edges, and delimited a 50-m radius circular plot around the station (Fig. S1C). Each census consisted in a 30 min observation slot, during which each individual bird heard or seen in the plot was counted and identified at the species level. Previous training, and the use of a plot map based on an aerial photograph, helped to accurately locate bird observations within the apple plantation and the hedgerows, even though woody cover. Bird individual movements and bird calls enabled to detect species even under conditions of low visibility due to dense foliage, within the 50-m radius distance. Perching habitat was also assessed for individual observations and assigned to apple plantation or surrounding woody hedgerow. Observations of birds performing high (> 25 m height) and non-stop flights over the sampling station were discarded. Censuses were performed from 7.30 AM to 12:30 PM avoiding days of rain and wind, every two weeks from August 2019 to July 2020, and by a single observer (DG).

2.4. Fruit counts in hedgerows

We established four fixed transects per orchard with lengths from 40 to 90 m along edges (Fig. S1C). Each transect was walked recording the occurrence of non-crop plants bearing fleshy fruits, identifying the species and visually estimating, for each individual plant, a Fruit Abundance Index (FAI) based on a semi-logarithmic scale (FAI: 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10000; 5 > 10000). Values of individual fruit production were later extrapolated from FAI ranks considering an allometric fit between actual values of fruit abundance and FAI values (Martínez and García, 2017). Fruits counts were done fortnightly from August 2019 to July 2020. For each fruiting species, a sample of 50 fruits (10 fruits from 5 plants) was taken across the different sites, to measure fruit diameter and length from fresh fruits in the laboratory.

2.5. Molecular and bioinformatic procedures

We analyzed DNA content from a subset of bird fecal content samples, chosen to represent different bird species according to their frequency of capture, as well as to cover different capture sites and dates across the whole year (Table S1). We extracted DNA from fecal samples using a silica solid phase protocol, following a modification of the methods described by Longmire et al. (1997) and Rohland et al. (2010). Briefly, samples were incubated overnight with Longmire (BE) and MixPK buffers at 37°C. Next, samples were centrifuged 2 min at 9600 g and supernatant was transferred to clean tubes. DNA was adsorbed to 80 µl silica per sample using a high guanidine thiocyanate salt concentration buffer. Low pH conditions were maintained by the addition of 90 µl of sodium acetate 3 M. DNA adsorbed to the silica was profusely washed with Wash Buffer (ethanol 50%, 0.01 M Tris-HCL pH 8, 0.001 M EDTA pH 8, and 0.125 M NaCl). Next, samples were loaded onto empty spin columns and DNA was recovered by centrifugation at 16,000 g using 60 µl of TE buffer.

In order to identify the species present in the DNA samples, 184 base pair (bp) fragments of the ribulose-bisphosphate carboxylase (rbcL) chloroplast gene for plants, and 178 bp of the cytochrome c oxidase subunit 1 (COI) mitochondrial gene for animals were amplified in two reactions using the primer pairs rbcL1 (5' TTG GCA GCA TTY CGA GTA ACT CC 3') / rbcLB (5' AAC CYT CTT CAA AAA GGT C 3') (Palmieri et al., 2009) and LepF1 (5' ATT CAA CCA ATC ATA AAG ATA TTG G 3')

(Hebert et al., 2004) / ZBJ-ArtR2c-deg (5' WAC TAA TCA ATT WCC AAA HCC HCC 3') (Shutt et al., 2020), respectively. Illumina sequencing primers were attached to these primers at their 5' ends. PCRs were performed in a final volume of 25 µl, containing 2.5 µl of template DNA, 0.5 µM of the primers, 12.5 µl of Supreme NZYTaQ 2x Green Master Mix (NZYTech), and 4 µl ultrapure water. The conditions were the following: an initial denaturation step at 95 °C for 5 min, then 35 cycles of denaturing at 95 °C for 30 s, annealing at 49 °C for 45 s, and extension at 72 °C for 45 s, followed by a final extension step at 72 °C for 7 min. Individual barcodes were attached in a second PCR round with identical conditions except for the number of cycles, only 5, and the annealing temperature at 60 °C. Library size was verified in 2% agarose gels and libraries were purified using the Mag-Bind RXNPure Plus magnetic beads (Omega Biotek). Then, they were quantified using Qubit dsDNA HSAssay (Thermo Fisher Scientific) and pooled equimolarly. Finally, the pooled library was purified and sequenced on an Illumina NovaSeq platform (PE250).

The quality of demultiplex raw files was checked with the software FastQC (Andrews, 2010) and Illumina adaptors were detected. These adaptors were trimmed using CUTADAPT (Martin, 2011) and paired reads were merged with FLASH2 (Magoč and Salzberg, 2011). Filtering based on the length of the fragment (183–185 bp for rbcL and 170–190 bp for COI), the number of mismatches in the primers (up to 2), and the quality (Phred quality score ≥ 20) was applied. Then, sequences were dereplicated (-derep fulllength) using the VSEARCH bioinformatic tool (Rognes et al., 2016) and de novo chimera detection was carried out using the UCHIME algorithm (Edgar et al., 2011) implemented in VSEARCH. Finally, sequences were clustered for plants with the SWARM algorithm (Mahé et al., 2015) with a d value of 1, and for invertebrates at a similarity threshold of 98% (-cluster fast, -centroidsoption) following Shutt et al. (2020).

Identification of sequences was based on the establishment of Operational Taxonomic Units (OTUs) using the script classify-consensus-vsearch implemented in Qiime2 (Bokulich et al., 2018) and the VSEARCH algorithm (Rognes et al., 2016) with a sequence similarity threshold of 90%. Databases for the taxonomic identification of the sequences were: for plants Bell et al. (2017) and for arthropods Robeson et al., (2021). Singletons (i.e., OTUs containing only one member sequence in the whole data set), OTUs occurring at a frequency < 0.1% in each sample, and unassigned OTUs were removed. In addition, from animal sequences only taxa within the phyla Arthropoda were selected.

2.6. Interaction data processing and analysis

2.6.1. Bird-pest interaction matrix

DNA-metabarcoding data from all sites and dates were pooled to assess the frequency of occurrence of different arthropod species on individual fecal samples of different bird species. Depending on the assigned taxonomic identities, arthropod preys were classified into different functional trophic groups (apple pest, predator, omnivore, parasitoid, other herbivore, detritivore, pollinator, and other) based on a thorough literature survey (e.g. Alford, 2007; Marshall, 2012; Albouy and Richard, 2017). For apple pest, we assumed an inclusive classification and considered all phytophagous species described to attack apple plants in at least one bibliographic source. All different OTUs assigned to a given apple pest species within an individual fecal sample were considered together, as a single occurrence of that pest species in the fecal sample. Thus, we assessed the presence/absence of different apple pest species on different individual samples across bird species. We considered each different bird-pest species pair as a bird-pest interaction, and each occurrence of a given pest species in a given bird individual sample as a bird-pest interaction event. We finally built a bird-pest interaction matrix whose cells contained the total number of occurrences of pest species per bird species (i.e. the sum of each pest species' occurrences across the fecal samples of each bird species). This occurrence-based method enabled to build a weighted network (i.e. a

network where different interactions show different frequency-based weights) while avoiding biases associated to a direct consideration of the number of DNA reads within and across bird samples (Deagle et al., 2019).

Some of the apple pest occurrences detected through DNA-metabarcoding in bird feces could correspond to secondary consumption by birds, that is, the consumption of an arthropod predator which had previously consumed an apple pest arthropod (Deagle et al., 2019). To assess how far our data could be affected by this phenomenon, we estimated the degree of co-occurrence of predators (e.g. spiders) or omnivores (e.g. ants) and apple pest species in bird individual fecal samples, as well as how many of these co-occurrences could be considered as secondary predation, as judged by a high relative read abundance (>1%) of predator sequences together with a low relative read abundance (<1%) of apple pest (Deagle et al., 2019; Mata et al., 2021). We found that predators/omnivores co-occurred with apple pests in 18.1% from 546 bird individual fecal samples. From these co-occurrences, only 2.9% were considered potential secondary predation. We, therefore, assumed that secondary predation had a negligible effect for the assessment of bird-pest interactions from our dietary dataset.

2.6.2. Bird-plant interaction matrix

To detect bird-plant interactions, we searched for the occurrence of fleshy-fruited species on individual regurgitation or fecal samples of bird species at two methodological stages. First, we identified the seeds of fleshy-fruited plants regurgitated or defecated by birds in field samples, both those collected in plastic bands placed beneath birds captured on mist nets, and those further detected in mist-netting bags. The species identification of intact seeds of fleshy-fruited species was confirmed from external morphology by comparison with an own seed reference collection from the study area and a published seed guide (Torroba-Balmori et al., 2013).

Second, we detected plant species in bird fecal samples through DNA-metabarcoding. Depending on the assigned species identities, plant OTUs were first classified into fleshy-fruited or non-fleshy-fruited species, based on a regional catalogue of vascular plants (Fernández-Prieto et al., 2014). The different OTUs assigned to the same plant species within a given individual fecal sample were considered together as a single occurrence of that plant species. Thus, we assessed the presence/absence of different plant species across bird species. From this dataset, we conserved only plant occurrences assumed to represent actual seed dispersal, excluding those potentially due to accidental or non-mutualistic plant tissue consumption by birds. For this, we firstly conserved plant occurrences assigned to bird species classified as legitimate seed disperser (i.e. those mutualistic frugivores typically swallowing fruits and further regurgitating or defecating intact seeds), excluding those assigned to bird species classified as pulp-pecker or seed predator (Simmons et al., 2018; Table S1). Thereafter, phenological and morphological matches between plant and bird species were verified for all assignments in order to exclude forbidden interactions (Olesen et al., 2011) that could reveal interaction misidentification. Phenological match was considered when the sampling date (i.e. bird capture date) occurred within the fruit ripening period of the plant species (span from the earliest to the latest observation date of ripe fruits across sites, expanded one week from both ends). Morphological match checked the fit between fruit size and individual bird gape width. We estimated fruit diameter from average diameter of fresh fruits, and bird gape width from field measurement. We considered a morphological match when the difference between mean fruit diameter and gape width was smaller than 0.5 mm, potentially enabling fruit swallowing. All plant occurrences classified as phenological, or morphological mismatches were discarded from the final dataset.

Once bird-plant species combinations were obtained from plant occurrence in seed dropping samples and/or DNA-metabarcoding, we considered each different combination of bird-plant species pair as a

bird-plant interaction, and each occurrence of a plant species in an individual bird sample as a bird-plant interaction event. We summed bird-plant interaction events emerging from field and DNA-metabarcoding procedures, avoiding the duplication corresponding to those events detected in the same individual birds by, consecutively, seed dropping samples and DNA-metabarcoding (Quintero et al., 2022). We finally built a bird-plant interaction matrix whose cells contained the frequency of occurrence of plant species per bird species, estimated by summing the data of occurrence of each plant across individual samples of each bird species.

2.6.3. Rarefaction analysis

We sought to evaluate the reliability of our sampling and dataset for representing the richness of species and interactions. For this, we built richness rarefaction curves based on Hill numbers for bird and pest/plant species, and for bird-pest and bird-plant interactions in the respective matrices. We used the function “iNEXT” from the package iNEXT (Hsieh et al., 2016) with 1000 bootstraps and built both richness and sample coverage curves considering a sampling-unit (mist-netting days, $N = 69$) incidence-frequency data. Analysis was performed with R statistical software (v 4.2.2; R Core Team, 2022).

2.6.4. Bipartite network analysis

Based on bird-pest and bird-plant interaction matrix, we analyzed the structure of respectively, pest-control and seed-dispersal bipartite networks. For each network, we estimated modularity (M), complementary specialization (H_2'), and nestedness (WNODF), using the R package bipartite (Dormann et al., 2009). Modularity value and individual modules within each network were estimated using the LPAwb+ algorithm, run 1000 times for each calculation (Beckett, 2016). The significance level of network parameters was tested against 1000 networks generated by the null model r2dtable (function nullmodel in bipartite) based on the Patefield algorithm and using z-score tests (Dormann et al., 2009). Null-model generated networks also enabled to represent network parameters as Δ (delta)-estimates (i.e. the difference between the raw value and the mean of null-model values), used to compare pest-control and seed dispersal networks irrespective of size differences. In the case of nestedness, we aimed to increase the robustness for estimating significance by using three different and complementary null models (CRT, Conserve Row Totals; CCT, Conserve Column Totals; and RCTA, Row Column Total Average; bird species as rows, pest/plant species as columns), implemented in FALCON (Beckett et al., 2014) in R.

2.6.5. Species centrality in hybrid network

We aimed to represent how the ecosystem services of pest control and seed dispersal may be combined through bird species acting as both pest predators and seed dispersers. For that, we represented a hybrid network emerging from pooling the bird-pest and bird-plant matrices (see Morrison et al., 2020, for a similar approach). Previously, we estimated relative interaction frequencies within each matrix, by dividing the frequency of occurrence of each paired interaction by the total number of interaction events in the matrix. We then applied a graph-theory approach in which bird, pest, and plant species are nodes and interactions between pairs of species are links (or edges) that have a quantitative score (relative frequency of interaction; Delmas et al., 2019). We estimated centrality to represent the topological relevance of bird species in the hybrid network, by means of three metrics: degree, closeness, and betweenness (Delmas et al., 2019). Degree centrality represents the importance of a node according to its number of links. Given that different links may have different weights (relative frequencies of interactions), we used a weighted degree, estimated as the sum of interaction frequencies of all links of a node. Closeness centrality measures the proximity of one node to all other network nodes, representing how efficiently a node is likely to influence the overall network. We used a measure of harmonic closeness, which considers the existence

of interaction restrictions between nodes (e.g. between pests and plants). Betweenness centrality describes the number of times a node occurs between a pair of other nodes, i.e. how many paths (either directed or not) go through it. We used the software Gephi 0.9.7 (Bastian et al., 2009) for network visualization and centrality measures computation (Yihan Hu algorithm; Hu, 2011).

2.6.6. Other statistical analysis

To explain the topological role of bird species in the hybrid network of pest control and seed dispersal, we related centrality measures (degree, closeness and betweenness, as response variables of independent models) to three ecological correlates of bird species: relative abundance, body size and diet diversity. Relative abundance was estimated as the proportion of total observations (number of individuals) accounted for each species in bird censuses, pooling the data from sites and dates. Bird body size was obtained from Dunning Jr (2008). Diet diversity (a measure of dietary generalization based on dominance in dietary items) was estimated through the inverse Simpson's Index ($S = 1/\sum p_i^2$) applied to the proportions (p) of different food types (i ; e.g. invertebrates, scavenging, fruits, nectar, ...) from EltonTraits 1.0 dataset (Wilman et al., 2014). We built different Generalized Linear Mixed Models (GLMM) using each centrality measure as a response variable, and all ecological correlates as fixed predictors standardized prior to analysis. To control the effect of statistical non-independence due to taxonomic affinity between species in the bird assemblage, we included bird genus and family identities as random factors with nested categories. Gaussian (identity link, log-transformed data) and Gamma (log link) distribution families were considered in separate models of all response variables, choosing the best-fit model of each response variable according to the inspection of the distribution of residuals against fitted values. All models were fitted using the R package lme4 (Bates et al., 2015). Conditional and marginal R^2 values (Nakagawa and Schielzeth, 2013) were obtained with the R package MuMIn (Barton, 2022).

3. Results

3.1. Bird sampling

Mist-netting led to the capture of 41 bird species (1070 individuals; Table S1), from which 1016 individual dropping samples were obtained across sites (Bustariega: 23.1% of samples; Camoca: 32.4%; Sorribes: 44.5%). The percentage of dropping sampled per month varied from 1.8% in March 2020–15.0% in December 2019. Mean number of dropping samples per bird species was 24.78 (± 7.29 SE). Bird censuses detected 910 individual birds belonging to 34 different species (Table S1), from which 41.4% were detected within the apple plantation and 58.6% in the woody hedgerows surrounding orchards.

3.2. Sequencing output

A total of 550 fecal samples were sequenced, with an average DNA concentration of 3.87 ng/ μ l (ranging from 86 to 0.03 ng/ μ l). Regarding arthropods, we obtained an average of 25,686 raw reads per sample (ranging from 17 to 131,033 reads) that dropped to 23,261 reads after filtering (from 48 to 118,698). Six samples were discarded during the filtering process; hence, we analyzed 544 samples obtaining over 3900 OTUs. Regarding plants, we obtained an average of 37,540 raw reads per sample (ranging from 50 to 192,616 reads) that dropped to 35,775 reads after filtering (from 41 to 185,641). No sample was discarded, hence, we analyzed 550 samples obtaining 955 OTUs.

3.3. Bird-pest and bird-plant interactions

Bird-pest interactions were detected in 184 individual bird samples (33.9% of DNA-metabarcoding bird samples) from 23 bird species. Bird-pest matrix included 49 pest species, 163 bird-pest interactions, and 293

interaction events (Fig. S2A). The percentage of pest species consumed was higher in *Parus major* (51.0%), *Sylvia atricapilla* (48.9%) and *Eri-thacus rubecula* (28.5%) and these bird species also accounted for the highest percentages of bird-pest interaction events (24.2%, 13.6%, and 12.3%, respectively; Fig. S2A). *C. pomonella*, *P. heparana*, and *Empoasca decipiens* were the pests more frequently found across bird species, whereas *C. pomonella*, *P. heparana* and *Hypomecis punctinalis* accounted for the highest percentages of interaction events (9.8%, 5.4%, and 5.4%, respectively; Fig. S2A). Cumulative curves and asymptotic estimates of richness indicated that 93.5% of birds, 87.3% of pests, and 32.9% of interactions were recorded (Fig. S3). Sample coverage was 97.4% for birds, 95.1% for pests and 57.7% for interactions.

DNA-metabarcoding detected 1780 occurrences of fleshy-fruited plant species across 510 bird individual fecal samples. From these, 55.2% were assigned to bird species classified as legitimate seed dispersers, whereas 44.8% to pulp-pecker or seed-predator species. From the 983 occurrences assigned to legitimate seed dispersers, 394 (40.1%) represented phenological and/or morphological mismatches between the corresponding bird and plant species and were not kept for analysis. Finally, 589 (59.9%) DNA-metabarcoding occurrences of fleshy-fruited plants, detected across 276 individual bird samples (50.2% of original samples), were considered as potential seed dispersal interaction events. Field sampling and analysis of droppings content added, respectively, 51 and 57 samples of different individual birds dispersing seeds of fleshy fruited plants, leading to a total of 353 individual bird samples. Bird-plant interaction matrix accounted for 15 bird species, 25 plant species, 117 interactions, and 697 seed-dispersal interaction events (Fig. S2B). From all interaction events, 84.5% were detected in DNA-metabarcoding analysis, and 7.3% and 8.2% were added from, respectively, field sampling and dropping content analysis.

The percentage of plant species consumed was higher in *S. atricapilla* (80.0%), *E. rubecula* (68.0%), and *T. merula* (64.0%), and these bird species also accounted for the highest percentages of bird-plant interaction events (31.9%, 22.5%, and 17.6%, respectively; Fig. S2B). *R. fruticosus*, *S. aspera* and *Sambucus nigra* were the plant species occurring across more bird species (80.0%, 73.3%, and 66.6% of bird species, respectively). The plant species accounting for more interaction events were *R. fruticosus* (23.7%), *C. sanguinea* (10.4%), and *Hedera helix* (10.3%; Fig. S2B). Cumulative curves and asymptotic estimates of richness indicated that 71.7% of birds, 91.9% of plants, and 64.6% of bird-pest interactions were recorded (Figure S4). Sample coverage was higher than 90% for birds, plants, and bird-plants interactions, indicating wide sample completeness in all cases.

3.4. Pest-control and seed-dispersal bipartite networks

Pest-control and seed-dispersal networks differed in structure. Both networks showed a degree of modularity significantly higher than expected by random, but modularity value of pest control doubled that of seed dispersal (Table 1). In this sense, six modules were differentiated in the pest-control network, each one dominated respectively by *Aegithalos caudatus*, *S. atricapilla*, *Phylloscopus collybita*, *E. rubecula*, *Cyanistes caeruleus*, and *P. major* (Fig. 1A; Fig. S5). Specialization degree of both networks also differed significantly from random expectations, but it was two-fold higher in pest-control than in seed dispersal (Table 1). Finally, the degree of nestedness was higher in seed-dispersal network than in pest-control network, in which did not differ from random expectation (Table 1). In seed-dispersal network, highly generalist avian frugivores such as *S. atricapilla*, *E. rubecula*, and *T. merula* interacted with many plant species and were the main dispersers of those plants with very few interacting partners (Fig. 1B; Fig. S6). From the 26 different bird species involved in bird-pest or bird-plant interactions, 12 occurred in both pest-control and seed dispersal networks (Fig. 1A-B).

Table 1

Values of structural parameters of bipartite networks of pest control and seed dispersal by birds. The non-randomness of the values of all parameters was assessed with null models from which delta-values (Δ), z-scores and degree of significance (P) were estimated. Estimates from three different null-model types are shown for nestedness.

			Pest control	Seed dispersal
Modularity	M		0.382	0.183
	Patefield	ΔM	0.108	0.078
		z-score	8.316	8.603
		P	<0.05	<0.05
Specialization	No. Modules		6	4
	H2'		0.309	0.148
	Patefield	$\Delta H2'$	0.132	0.086
		z-score	8.969	12.686
Nestedness		P	<0.05	<0.05
		WNODF	18.058	51.689
	CRT	$\Delta WNODF$	-0.370	13.119
		z-score	-0.222	3.820
		P	0.578	0.001
	CCT	$\Delta WNODF$	-3.473	8.134
		z-score	-2.896	3.675
		P	0.996	0.0009
	RCTA	$\Delta WNODF$	-2.631	8.560
		z-score	-1.765	2.662
	P	0.962	0.0031	

3.5. Bird species centrality in hybrid network

The hybrid network considering bird, pest, and plant species as nodes, and paired interactions as links, enabled to represent the topological relevance of different species from their spatial position (Fig. 2). In this sense, species like *S. atricapilla* and *E. rubecula* occupied a highly central position in the global network and accounted for a large proportion of interaction events with both pest and plant species. Species like *T. merula* and *Turdus philomelos* occupied lesser central positions since even when presenting interactions with both pest and plant species, their interactions were skewed to seed dispersal. Finally, species such as *P. major*, *C. caeruleus*, and *A. caudatus*, were more peripheral even with moderate-to-high weighted degrees, given that they did not participate in seed dispersal.

Weighted degree, harmonic closeness, and betweenness varied strongly across bird species and were positively correlated among them (all Spearman correlation coefficients, $\rho \geq 0.90$, $P \leq 0.0001$; Fig. S6A). Gaussian-family GLMM offered a better fit than those based on Gamma family, for all the centrality measures used as response variables (Fig. S7; Table S3). The three centrality measures showed a similar pattern of response to ecological correlates across bird species. In all cases, centrality was positively affected by bird species relative abundance but independent of bird body size or diet diversity (Table 2, Fig. 3). All three fixed effects together accounted for more than 38% of

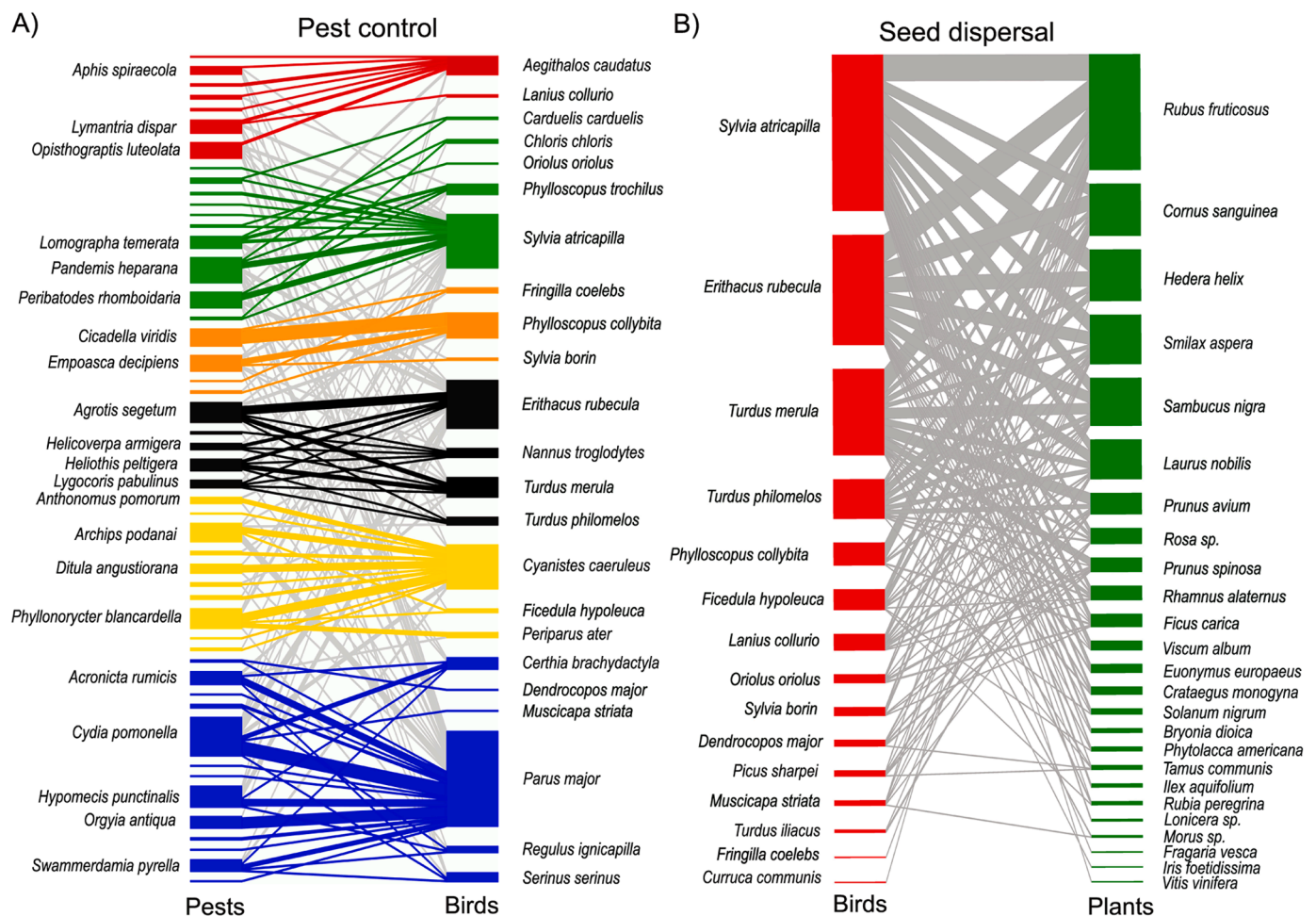


Fig. 1. Detailed representation of bipartite networks between (A) pests and birds (pest control), and (B) and birds and plants (seed dispersal). Rectangles in columns correspond to different species, with rectangle height being proportional to species interaction frequencies (pest species names are only quoted for those with interaction frequency $\geq 1.5\%$; see Fig. S5 for complete quotation). Links between rectangles represent paired interactions between species, with link width being proportional to the proportion of interactions. Species and interactions are ordered to highlight (A) modularity (different colors indicate species and links conforming different modules) and (B) nestedness.

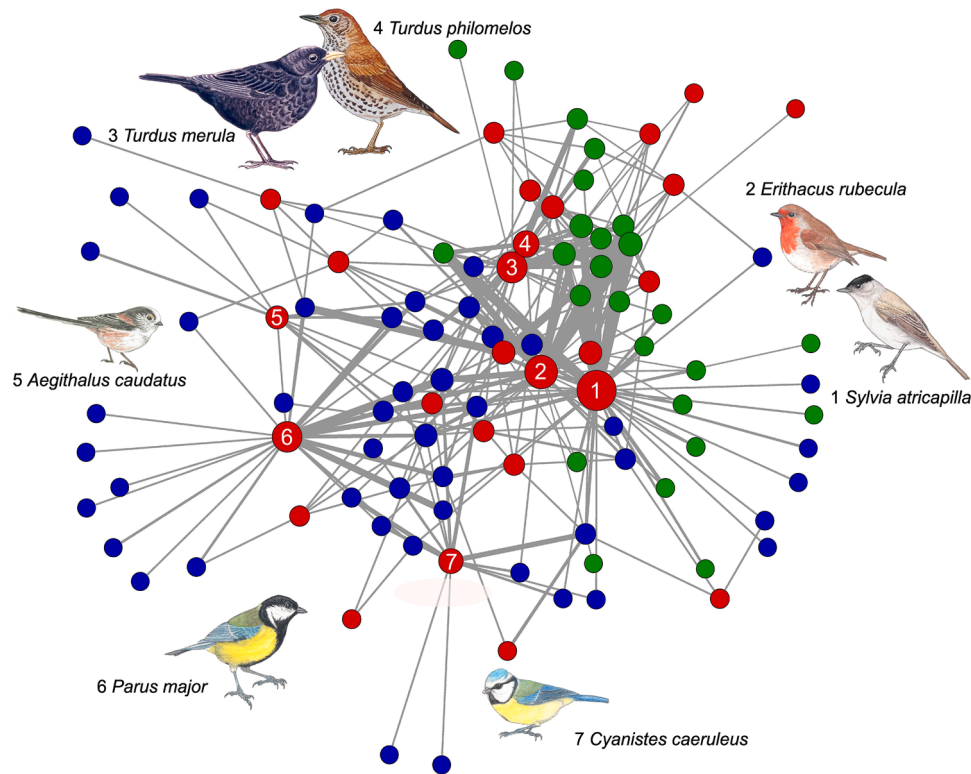


Fig. 2. Hybrid network graph representing different species (nodes, dot size proportional to weighted degree) of birds (red), pests (blue) and plants (green), interconnected through ecological interactions (grey links, width proportional to interaction frequency). Spatial visualization based on Yifan Hu algorithm. Different bird species are indicated through numbers, drawings and names to highlight central and peripheral positions. Artwork by Daniel García.

Table 2

Results of Generalized Linear Mixed Models evaluating the effects of bird species relative abundance (percentage of individuals), body mass (g) and diet diversity (inverse Simpson Index) on bird species centrality measures on the hybrid (pest control and seed dispersal) interaction network. Models considered a Gaussian (identity link) distribution family for log-transformed response variables. All predictors were standardized prior to analysis. Models included the variance (\pm SD) estimate for taxonomic identity factors included as random effects. Marginal and conditional (in parentheses) R^2 values are also given.

Response variables	Weighted degree				Harmonic closeness				Betweenness			
	Estimate	SE/SD	t	P	Estimate	SE/SD	t	P	Estimate	SE/SD	t	P
	$R^2 = 0.750 (0.832)$				$R^2 = 0.619 (0.682)$				$R^2 = 0.381 (0.381)$			
Predictors												
Intercept	0.029	0.005	5.09	<0.001	0.151	0.003	41.06	<0.001	1.685	0.139	12.12	<0.001
Relative abundance	0.041	0.005	8.48	<0.001	0.022	0.003	6.18	<0.001	0.606	0.161	3.77	0.0011
Body mass	0.0003	0.005	0.06	0.953	-0.0005	0.003	-0.15	0.886	-0.084	0.142	-0.59	0.560
Diet diversity	-0.002	0.005	-0.39	0.699	-0.004	0.004	-1.06	0.299	-0.157	0.162	-0.97	0.341
Genus [Family] (random)	0.000	0.000			0.000	0.000			0.000	0.000		
Family (random)	0.0001	0.013			0.0001	0.007			0.000	0.000		

the variability in all centrality measures, as judged by marginal R^2 values in all models.

4. Discussion

Agroecosystem sustainability depends on the multiple ecosystem services provided by biodiversity, their trade-offs and synergies (Power, 2010). Most of these services emerge from ecological interactions between cultivated and wild organisms, whose singularity and complexity are now affordable through network science (Allen et al., 2022; Windsor et al., 2022). Here, we applied a network approach to disentangle, for the first time, how pest control and seed dispersal are bound together in agroecosystems. By using DNA-metabarcoding, we identified natural enemy-pest and seed disperser-plant interactions simultaneously driven by wild birds in cider apple orchards across a whole year. According to the respective antagonistic and mutualistic typologies of interactions, we found strong structural differences between pest-control and seed-dispersal networks, with potential consequences for the

functioning of ecosystem services. We pooled together interactions in a global hybrid network, finding strong heterogeneity across bird species in their relative role to connect pest-control and seed-dispersal services. Such a role mostly depended on the relative abundance of bird species in apple orchards and was unaffected by other ecological features. Our findings, thus, highlight the relevance of common bird species for the provision of ecosystem services bundles in agroecosystems.

4.1. Structure of pest-control and seed-dispersal networks

The present study of ecological networks relies on the monitoring of trophic interactions between birds and arthropods, and birds and plants, mostly assessed through the detection of prey DNA-remains in bird fecal samples. As with other methodologies for monitoring trophic interactions (e.g. Quintero et al., 2022), our species-specific estimates may suffer from detectability biases affecting both consumer and prey species. In the case of birds, mist-netting methodology may impose under-representation of species with specific movement and behavioral

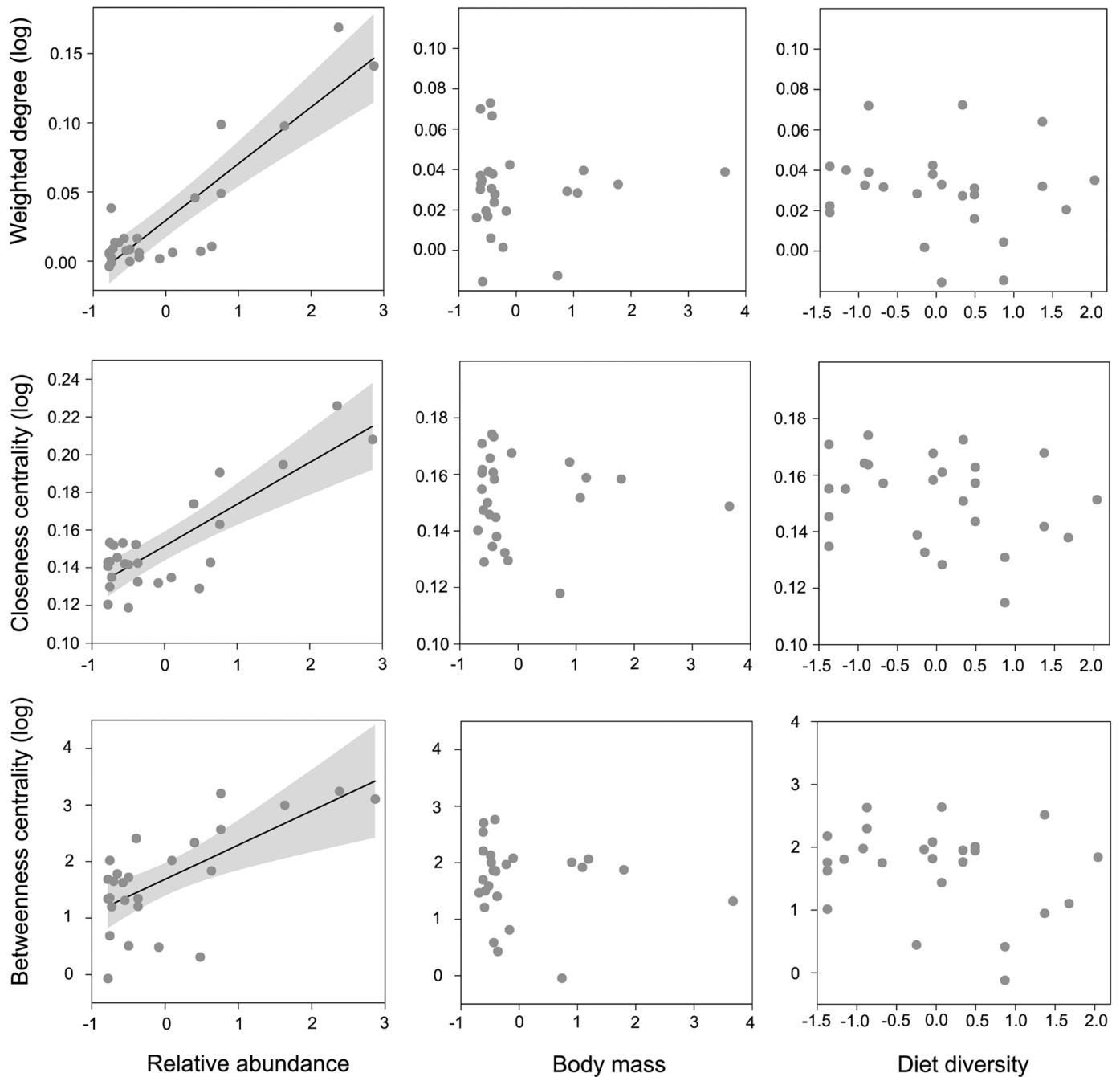


Fig. 3. Relationships between relative abundance, body mass, and diet diversity, and centrality measures (weighted degree, harmonic closeness and betweenness) predicted by Generalized Linear Mixed Models. Dots represent different bird species. Linear fits of significant partial effects, with confidence bounds and fitted values, are shown.

patterns (e.g. air-dwelling species, such as swallows, whose flights are usually higher than the apple canopy height, but still they are known to control pests in other crops; García et al. 2023). In the case of pests and plants, DNA-metabarcoding techniques may be affected by species-specific detection biases, related to the differential degree of degradation of DNA in consumer gut or to the amplification ability of universal DNA-primers for different biological taxa (Deagle et al., 2019). Even under-representing some bird-pest/plant interactions, some of them known in our system (e.g. *C. caeruleus* frequently consumes the rosy apple aphid *D. plantaginea*, García et al., 2021), we consider our methodology robust enough for inferring the global structure of ecological networks. Concerning bird species, our sampling was highly representative of the relative abundance of species in the bird

assemblage, as evidenced by the strong correlation between census-based abundance and mist-netting occurrence (Pearson's correlation coefficient: $r = 0.885$, $P < 0.0001$, $N = 45$ species across censuses and mist-netting). Concerning pest and plant species, the high values of sample coverage estimated from cumulative curves (Figs. S3 and S4) indicated that few interactions with unsampled pest or plant species were left to describe.

We found different topologies in the networks underpinning pest-control and seed-dispersal services. As shown in other antagonistic, predator-prey networks (e.g. Mata et al., 2021; Suzuki et al., 2023), bird-pest interactions led to modularity and specialization levels higher than expected by random. This result indicates that, even with some overlapping across birds in the pests occurring in their diets (see grey

colored links in Fig. 1A and Fig. S5), there were well defined clusters (i.e. modules) of interactions between groups of birds and pests. Interaction clusters, in any case, were characterized by the occurrence of a dominant bird species, which accounted for a disproportionately high frequency of interactions with pests. In addition, the specialization degree of pest-control network ($H_2' = 0.309$), even being relatively low (H_2' value ranges from 0 to 1) was similar to other pest-control networks driven by vertebrates (e.g. bats, Mata et al., 2021). Moreover, our results of differential pest consumption by different bird species (e.g. *C. caeruleus* and *P. major*) are consistent with our previous findings based on the identification of prey brought to nestlings in nest-boxes in cider apple orchards (García et al., 2021). Importantly, the trophic niche segregation between bird species evidenced here suggests a high degree of functional complementarity, even between taxonomically close species (e.g. the Paridae *P. major*, *C. caeruleus*, and *A. caudatus* belonged to different network modules; Fig. 1A; Fig. S5). A major consequence of this complementarity could be positive effects of bird biodiversity in the magnitude and stability of pest-control service, as previously suggested for this system (Martínez-Sastre et al., 2020; Peña et al., 2023a).

Different mechanisms may underpin bird segregation in pest consumption. On the one hand, bird morphological and behavioral differences may lead to different small-scale foraging patterns (Carrascal et al., 1990), facilitating the encounter with different pest species in apple orchards. For example, foliage-gleaning birds such as *C. caeruleus* may easily access to pests on leaves or shoots (e.g. aphids; García et al., 2021), whereas bark-gleaning birds like the treecreeper *Certhia brachydactyla* may feed on pests in bark crevices (e.g. *C. pomonella* in diapause cocoon stage; Solomon and Glen 1979). On the other hand, phenological differences in the distribution of abundances of both predators and preys may also underlie interaction segregation patterns observed in a compiled, whole-year network (Suzuki et al., 2023). In our case, migration and wintering dynamics of passerines (e.g. González-Varo et al., 2021), and population growth and diapause cycles of arthropods (e.g. Pak et al., 2019), are strong sources of temporal heterogeneity in the probability of encounter between birds and pests. Further analysis considering explicitly the timing of interactions across the year, and species morphological or behavioral traits, is now necessary to understand the specific causes of module organization and composition in the present pest-control network (Dormann et al., 2017).

The seed-dispersal network emerging from the studied bird-plant interactions was remarkably less modular and specialized than the pest-control one but was highly nested. Nestedness mostly emerged from the fact that highly generalist species accounted for interactions with many partners, including both generalist and specialist species (Bascompte et al., 2003). For example, *S. atricapilla* and *E. rubecula* represented super-generalist species interacting, respectively, with 80% and 68% of the plant species. These included generalist species (e.g. *R. fruticosus*, *S. aspera*) and also plants with very few interacting partners (e.g. *Ilex aquifolium*, *Rubia peregrina*; Fig. 1B and Fig. S2B). From the side of plants, *R. fruticosus* and *S. aspera* were at the core of the nested structure, as they interacted with 75% and 69% of the bird species, including unusual ones such as *Curruca communis* and *Turdus iliacus* (Fig. S2B). The shown patterns of generalization and nestedness may have relevant consequences for the functioning of the seed-dispersal service. Namely, widening the number of interacting partners may represent an ecological insurance enabling bird or plant species to maintain functional contributions in the case of partner population decay or extinction (Blüthgen and Klein, 2011). We thus expect to have a seed-dispersal service resilient to population oscillations associated, for example, to interannual dynamics of bird wintering or fruit masting (García et al., 2013).

Generalization and nestedness in the studied seed dispersal network may emerge from several non-exclusive sources. First, generalization increases when species traits do not impose general barriers for interaction and thus facilitate relationships among many different partners (Peralta et al., 2020). This seems to be the case for both bird and plant

species in the studied system. For example, the medium-to-large gape width values of most birds (e.g. species average in mm; *S. atricapilla*: 10.2; *E. rubecula*: 10.7; *T. merula*: 15.8) gave access to a high variety of fruit sizes, whereas the small-to-medium fruit diameters of most plants (e.g. species average in mm; *R. fruticosus* drupe: 3.3; *C. sanguinea*: 6.3; *S. aspera*: 7.7) rendered berries easy to handle and swallow by most frugivores. Second, strong differences between species in relative abundance, and the concomitant probability of random encounter, may also foster dominant species to become super-generalist (e.g. birds *S. atricapilla*, *E. rubecula* Table S1; fruiting plants *R. fruticosus*, *H. helix* Table S2). This sort of dominance effect has been evidenced in other regional seed-dispersal networks that share a large part of the frugivore and plant assemblage with apple orchards (e.g. Peña et al., 2023a, b).

4.2. Connecting pest control and seed dispersal through a hybrid network

The occurrence of shared bird species in bird-pest and bird-plant interactions (12 from 26 bird total species, Fig. 1A-B) enabled us to build a hybrid network to highlight the common suppliers of both pest-control and seed-dispersal functions in apple orchard. Although measured here at the species level, this dual ecosystem service may even involve the same individual birds, as we found simultaneous consumption of pest arthropods and fleshy fruits in 18.02% of bird fecal samples in which pest-control or seed dispersal were detected ($N = 455$). The remaining cases corresponded to separate detections of pest control and seed dispersal across different individuals of the same species but frequently corresponding to similar dates.

The dual role of birds highlights their relevance in maintaining a complex and synergistic relationship between apple crop and semi-natural habitats within the agroecosystem. On one side, hedgerows and forest patches represent suitable habitats to support the populations of insectivorous birds that spill-over in apple orchards to exert top-down control on apple pests (García et al., 2018; Martínez-Sastre et al., 2020). These surrounding habitats provide protection against predators, nesting sites, and feeding resources, among which fleshy fruits are especially relevant during autumn and winter (Bouvier et al., 2020, 2022). After swallowing fruits, birds defecate or regurgitate many intact seeds of woody species, triggering not only the process of plant regeneration within seminatural habitats but also the colonization of unmanaged areas and the spontaneous recovery of hedgerows (Flinn and Vellend, 2005; Harvey, 2000). On the other side, apple orchards offer many arthropods that represent complementary foraging resources for insectivorous birds (Génard et al., 2017). There is, thus, a bird-mediated feedback of ecosystems processes between semi-natural woody habitats and apple orchards: hedgerows would facilitate pest control to apple orchards whereas apple orchards would contribute to preserve seed dispersal driving the long-term dynamics of hedgerow woody plants (see also Rey et al., 2021).

4.3. Determinants of bird species role in ecosystem services bundle

We used here a graph-theory approach to assess, through centrality measures, the contribution of different bird species to the global connectivity of bird-pest and bird-plant interactions and hence, to the bundle of pest-control and seed-dispersal ecosystem services. We found marked inequalities across bird species in their hybrid network role, with few central species acting as main connectors of ecosystem services (Fig. 2; Fig. S6B). This sort of inequality seems to be a general pattern in interaction network studies, both when ecological functions are considered alone (e.g. Bonfim et al., 2023) or in combination (e.g. Timóteo et al., 2023).

A reason of centrality differences among birds shown here is that a large part of insectivores had been discarded as seed dispersers, even when potentially interacting with fleshy-fruited plants through seed or pulp consumption (39.4% of plant species occurrences detected in initial DNA-metabarcoding dataset was assigned to pulp consumption or seed

predation, Simmons et al., 2018). Thus, these bird species (e.g. *P. major*, *C. caeruleus*) occupied more peripheral positions in the hybrid network even when accumulating a large proportion of interactions with pest arthropods. More importantly, our analysis of ecological correlations evidenced that bird centrality increased proportional to species relative abundance. Hence, very common species such as *S. atricapilla* and *E. rubecula*, recognized to have switching insectivore and frugivore diets (Carnicer et al., 2009), and also to be legitimate seed dispersers (Rumeu et al., 2023), were the main responsible of combining pest control and seed-dispersal services in apple orchards.

The positive relationship of centrality measures and abundance shown here suggests that, at least for birds, neutral processes would explain better than deterministic ones the combined functional outcome of the hybrid network (see also Timóteo et al., 2023). That is, a higher probability of encounter of pests and fruits with the most abundant, generalist bird species would drive the accumulation of the different ecological interactions on common birds (Peralta et al., 2020). An explicit consideration of natural abundances of pests and fleshy fruits (e.g. Peña et al., 2023b) would be, anyway, necessary for an accurate assessment of neutral effects in the occurrence of interactions. In any case, although we did not find evidence of body mass or diet diversity effects, we cannot exclude other ecological features such as explicit consumer-resource trait matching, behavior, and bird-bird interactions (Bartomeus et al., 2016) accounting for the significant amount of variance in centrality still unexplained by our models.

5. Concluding remarks

Our study highlights the relevance of common species for the maintenance of ecosystem services bundles, widening the previous research focused on single services (Gaston et al., 2018). This is especially relevant in agroecosystems, in which crop production and biodiversity depend frequently on the complex relationships between social and ecological processes (Allen et al., 2022; Windsor et al., 2022). In this sense, in a context of strong negative impact of agricultural management on bird conservation in Europe (Rigal et al., 2023), it seems relevant to point at common species as conservation targets, even though species like *S. atricapilla* or *E. rubecula* are currently increasing or maintaining their population sizes (Burns et al., 2021). Equally relevant is to promote management actions facilitating bird persistence. In this sense, orchard-scale measures like preserving hedgerows or adjacent forest patches in a large part of orchard edges and keeping high levels of apple canopy cover within orchards, have been identified to promote bird abundance and richness (García et al., 2018; Martínez-Sastre et al., 2020). Additional within-orchard actions of ecological intensification, such as the installation of nest-boxes, have been also shown effective to promote populations of insectivorous birds (García et al., 2021). Beyond orchards extents, administration-driven land management plans are also recommended. These should seek to maintain landscapes with high connectivity and threshold cover values of seminatural woody habitats (i.e. $\geq 20\%$; Garibaldi et al., 2021), including control of land consolidation programs and the promotion of passive rewilding or even active restoration of abandoned land. Importantly, all these kinds of actions are suitable to receive support under the current development of European Common Agrarian Policy 2023–2030 program (Díaz et al., 2021).

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Author statement

DG, BR and JCI conceived the ideas and designed methodology; DG, BR and MM collected field data; JCI and GP collected molecular data; DG analyzed the data; DG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Illera Juan Carlos: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Rumeu Beatriz:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing – review & editing. **García Daniel:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **González-Varo Juan Pedro:** Funding acquisition, Methodology, Writing – review & editing. **Palomar Gemma:** Data curation, Funding acquisition, Writing – review & editing. **Miñarro Marcos:** Data curation, Funding acquisition, Investigation, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Daniel García reports relationships with Fundación BBVA and Government of Principality of Asturias that include funding grants. Beatriz Rumeu, Marcos Miñarro and Juan Pedro González-Varo report relationships with Ministry of Science and Innovation of Spain that include funding grants.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.108927.

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