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Insectivore diet and abundance determine the contribution of bird species to services and disservices in an agricultural ecosystem

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ABSTRACT

Insectivorous birds provide an essential ecosystem service in agriculture by feeding on arthropods considered pests but can also consume arthropods considered to be natural enemies of such pests. Therefore, depending on the dietary composition of the birds, intraguild predation could outweigh pest control services. This study addressed the agronomic quality, defined as the trade-off between ecosystem services (pest control) and disservices (intraguild predation), of 26 insectivorous bird species in culturally and economically important cider apple orchards in northern Spain. We used DNA-metabarcoding techniques to analyze birds' diets. First, we examined whether the trophic position of bird species can be inferred from functional traits related to foraging and movement behavior and from the degree of insectivory in their diets. Then, we tested whether bird abundance and trophic position influenced agronomic quality, based on the proportion of arthropod crop pests and natural enemies in their diet. Finally, we combined bird abundance, insectivory, and agronomic quality to infer the potential contribution of each bird species to pest control. Bird trophic position was positively related to the degree of insectivory, with this effect being modulated by traits related to body size. The trophic position of birds was inversely related to their agronomic quality. Nevertheless, the agronomic quality only slightly affected the differential contribution of bird species to the whole assemblage effect. Overall, we found the potential of insectivorous bird species to control pests can be estimated based on their trophic position. Yet, in agroecosystems with uneven avian species abundance, the potential contribution of bird species to pest control services may be driven by their quantitative contribution rather than by the bird's per capita, qualitative effects. Finally, our results suggest that rare insectivorous birds may have a redundant role in pest control, due to the overwhelming functional dominance of common species.

Keywords: agroecosystems, DNA-metabarcoding, intraguild predation, northern Spain, pest control, trophic interactions

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LAY SUMMARY

- The impact of insectivorous birds on crops depends on whether they consume crop pests or the natural enemies of pests.
- We studied the diet of 26 insectivorous bird species in apple orchards in northern Spain, identifying arthropod prey species from DNA remains in bird feces.
- We calculated how many pests each bird species eats in relation to natural enemies and how much these bird species contribute to pest control.
- We found that bird species that consume relatively more arthropods as a part of their general diet also consume more natural enemy arthropods.
- The abundance of each bird species mainly determines its effect on pest control.

La dieta y la abundancia de aves insectívoras determinan su impacto en los servicios y diservicios en un ecosistema agrícola

RESUMEN

Las aves insectívoras desempeñan un papel clave en los agroecosistemas al alimentarse de plagas, aunque también consumen otros enemigos naturales de estas plagas, lo que condiciona su efecto neto sobre los cultivos. Evaluamos la calidad agronómica de las especies de aves, definida como el balance compensatorio entre el control de plagas (servicio) y la depredación intragremial (diservicio). Mediante técnicas de código de barras de ADN analizamos las dietas de 26 especies de aves insectívoras en plantaciones de manzano de sidra del norte de España, un cultivo de relevancia cultural y económica. Investigamos si el grado de insectivoría y las características funcionales relacionadas con la búsqueda de alimento permiten inferir la posición trófica de las aves. Además, exploramos cómo la abundancia y la posición trófica de las aves influyen en su calidad agronómica, medida a partir de la proporción de plagas y enemigos naturales en su dieta. Por último, combinamos abundancia, insectivoría y calidad agronómica para estimar la contribución potencial de cada especie al control de plagas. Nuestros resultados muestran que las aves más insectívoras tienden a ocupar posiciones tróficas más altas, siendo este efecto modulado por su tamaño corporal. Sin embargo, una posición trófica más alta se asocia con una menor calidad agronómica, lo que implica un mayor impacto negativo sobre los enemigos naturales de las plagas. Pese a ello, a calidad agronómica tiene un peso limitado en la contribución de las especies de aves al efecto global de la comunidad. Concluimos que la posición trófica predice el potencial de control de plagas de las especies de aves. No obstante, en sistemas con abundancias de especies desiguales, la contribución de cada especie depende más de su abundancia relativa que de su eficacia individual. Finalmente, nuestros hallazgos sugieren que las aves raras tienen un rol redundante en el control de plagas, mientras que las más abundantes dominan funcionalmente este servicio.

Palabras clave: agroecosistemas, ADN-código de barras, depredación intragremial, norte de España, control de plagas, interacciones tróficas

INTRODUCTION

Pest control ecosystem services in agriculture are frequently driven by the biodiversity of the pests' natural enemies (Dainese et al. 2019, Buzhdygan and Petermann 2023). A higher species richness of natural enemies in crops is expected to foster pest control through an increased probability of incorporating functionally dominant species (i.e., sampling effects) or by promoting the additive effects of functionally complementary species (i.e., niche complementarity effects; Letourneau et al. 2009, Snyder 2019). Generalist predators of different taxa (e.g., birds, bats, and arthropods) can occupy different trophic niches and complement each other's actions against pests. These insectivores feed on a variety of species and life stages and show daily and seasonal variations in the foraging niche breadth (Remmel et al. 2011, Maas et al. 2016, Vansynghel et al. 2022). Such complementarity may facilitate the efficient response of insectivores to pest outbreaks (Garfinkel and Johnson 2015, Snyder 2019). Nevertheless, in the case of birds performing as natural enemies of pests, it is well known that birds may also forage on other predatory species, such as arthropods, releasing pests from their actual major controllers (e.g., Grass et al. 2017). This sort of intraguild predation by birds on mesopredatory arthropods, which also act as natural enemies of the pest species (hereafter referred to simply as "natural enemies"), can counteract and in some cases even exceed the positive impacts of biodiversity on pest control, thereby resulting in net ecosystem disservices (Martin et al. 2013, Pejchar et al. 2018). Despite this, little is known about the mechanisms that underpin the trade-offs between ecosystem services-disservices (ES-ED; see Prigioniero et al. 2022 for similar terminology) involving bird intraguild predation and pest control (but see Pejchar et al. 2018, Garcia et al. 2020).

An explicit approach of trophic cascades in agroecosystems, accounting for the outcomes of different interactions among birds, other natural enemies, and pests, may elucidate ES-ED trade-offs in crops (Mooney et al. 2010, Karp and Daily 2014). In this sense, classifying bird species based on their trophic position may help to assess their role in the mentioned trade-off. Trophic position can be estimated from the rank of the species in the trophic chain, or from the proportion of prey they consume that have mesopredatory and phytophagous habits (e.g., Karp and Daily 2014, Garfinkel et al. 2022). This sort of approach requires the identification of the different prey taxa consumed by birds (e.g., by means of genetic or isotopic techniques; Garfinkel et al. 2022, Otieno et al. 2023), and also the assessment of a trophic position (whether primary or secondary consumer) for these prey species. From an agronomic perspective, the utility of estimating the trophic position of birds is questionable when the mesopredatory and phytophagous prey in their diet do not represent actual natural enemies or pests of the target crop. Assessing the role of birds by means of parameters explicitly accounting for the proportions of crop pests and arthropod natural enemies in their diets can translate ecological inference into agronomic information (Garfinkel et al. 2022). These parameters could inform the agronomic quality of birds, helping farmers to identify which species provide more ecosystem services and fewer disservices. Finally, understanding determinants of both trophic position and agronomic quality, such as species traits (Philpott et al. 2009, Luck et al. 2012), and species abundances (Gaston et al. 2018, García et al. 2024) can also be informative.

After assessing the roles of individual bird species in ES-ED trade-offs, the potential contribution of these bird species needs to be interpreted relative to the whole bird assemblage, depending on both the per capita species effects and their relative abundances (Schupp et al. 2010, Pejchar et al. 2018, Smith et al. 2022). Potential contributions will inform us about whether the pest control services ultimately depend on a few dominant species (with many other species being redundant) or, conversely, on the additive and complementary contribution of the different bird species.

Here, we focus on insectivorous birds that visit orchards in northern Spain. Apple (*Malus x domestica* Borkh.) is the most important fruit crop in Europe (Eurostat 2024) and the third most important in the world (FAOSTAT 2024). In northern Spain, almost all apple crops are devoted to the production of cider. This alcoholic drink produced from fermented apple juice is a highly valuable product in cultural and economic terms (e.g., it has a Protected Designation of Origin). Importantly, cider apple orchards host a species-rich assemblage of insectivorous birds that represent a group of generalist predators known to control apple pest arthropods (García et al. 2018, Martínez-Sastre et al. 2020a). These insectivorous birds, however, may also exert intraguild predation on arthropods that act as natural enemies of economically harmful arthropods (García et al. 2018, 2021).

As a general objective, we address how the insectivore diet and the ecological features of species condition the trade-off between ecosystem services and disservices, and how the trade-offs operating at the bird species level scale up to the bird assemblages. We use DNA-metabarcoding techniques

to characterize the trophic position and agronomic quality of 26 bird species in apple orchards. Specifically, we seek to evaluate (1) whether the trophic position of a bird species is a function of its functional traits, (2) if bird species abundance and trophic position determine the agronomic quality of the species, and (3) if the relative contribution to pest control service varies among bird species and whether it is affected by diet. We expect that (1) some functional features, such as morphology (e.g., Luck et al. 2012), will affect the relative proportions of arthropod types consumed by each bird species; (2) birds in a higher trophic position (i.e., consuming a larger proportion of predatory than phytophagous arthropods; Garfinkel et al. 2022) will have a lower agronomic quality; and (3) different bird species will contribute unequally to the pest control service depending on their insectivore diet but also on other features, such as abundance (e.g., García et al. 2024).

METHODS

Study System

In the region of Asturias in northern Spain (Supplementary Material Figure 1), Western Europe, local cider apple cultivars are tolerant to common apple diseases such as scab, canker, or powdery mildew. The most important arthropod pest for cider apples is *Cydia pomonella* (codling moth), which attacks the fruits. Aphids (*Dysaphis plantaginea*, *Aphis* spp., and *Eriosoma lanigerum*) and *Anthonomus pomorum* (apple blossom weevil) may be of particular concern in some orchards and years (Miñarro et al. 2011). Aesthetic damage is not important for cider production, so the cultural tolerance of growers to pests is generally high, leading to scarce, or even no use of insecticides in some orchards. Agricultural intensification in orchards and the surrounding landscape is low. Indeed, orchards are usually embedded in a highly variegated landscape with frequent patches of semi-natural habitats, enabling highly diverse communities of arthropods and birds to exist (Miñarro et al. 2011, Martínez-Sastre et al. 2020a).

Field Sampling

To characterize bird diets, we conducted a field study in 3 apple orchards consisting of trees of several local cultivars with a mean density of ~500 trees ha⁻¹ grown on semi-dwarfing rootstocks. Apple orchards were 0.8, 1.4, and 5.3 ha in size, separated by at least 1.5 km, and were embedded in a bocage-type landscape with a semi-natural woodland habitat cover ranging between 22% and 28%, comprising small forests, isolated trees, hedgerows, and shrubland patches (Supplementary Material Figure 1A and 1B).

We conducted 30-min point counts at one sampling location in each of the 3 orchards, 25 m away from orchard edges, twice a month from August 2019 to July 2020 (total: 24 surveys per orchard). If meteorological conditions permitted, the 3 orchards were surveyed in succession on the same morning. To prevent temporal biases, the order of visits to the orchards was randomly selected for each set of surveys (i.e., every fortnight). Surveys were conducted by a single observer, beginning no earlier than 0730 hours and concluding no later than 1230 hours in the afternoon. The observer identified species and counted all individuals heard or seen in a 50-m radius from the sampling location (Ralph et al. 1995). 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 adjacent hedgerows despite the presence of woody cover. Bird individual movements and bird calls allowed species to be distinguished even under conditions of low visibility due to dense foliage, within the 50-m radius distance. We also recorded the type of the perching habitat using 2 well-defined categories: (1) surrounding woody vegetation and (2) apple tree plantation. When possible, we discarded repeated observations attributable to the same individual that had remained in the plot during a given observation period (e.g., individuals that appear intermittently at the same perching site within short time periods). Birds observed to be flying at an altitude exceeding 50 m without making any stops at the sampling location were not considered. To characterize the bird assemblage, we grouped the data from the 3 orchards and estimated the relative abundances of birds as the cumulative number of individuals recorded across all orchards and surveys over a year. We assume that this bird abundance metric might, despite our efforts, include some repeated counting of individual birds, and thus it must be considered as an estimate of bird activity across sites in functional terms, rather than a measure of local bird population sizes.

In the same period of surveys, we captured birds with mist nets and collected fresh fecal samples, following a common methodology in mist-netting studies (Parrish et al. 1994, Karp et al. 2013). For each session, we placed two 9–18-m long and 2.5–3-m high mist nets with a mesh size of 16 × 16 mm (total capture area of 178.5 m²) inside the apple plantation and 3 nets at plantation borders (as bird activity is usually higher there), 2 m from woody hedgerows (Supplementary Material Figure 1C). Nets were set just before dawn and removed around noon, remaining open for 5 consecutive hours and checked for bird captures every 45–60 min. Captured birds were kept up to 40 min inside clean ringing cloth bags to collect feces. Cloth bags were sterilized after every ringing session by machine washing them with bleach. All captured birds were marked with a uniquely numbered aluminum ring. We weighed each bird to the nearest gram, and measured wing length, tarsus length, and gape width to the nearest millimeter. We collected fecal samples from the cloth bags using sterile swabs and stored them in the field at 4°C until final storage at –20°C in the laboratory.

Molecular and Bioinformatic Procedures

We selected ~50% (*n* = 550) of the fecal samples collected for molecular analysis, ensuring that different bird species were represented according to their frequency of capture (avoiding species with fewer than 3 samples; *n* = 26), and that the 3 capture sites and 12 months of the survey were covered. We extracted DNA from the samples using a silica solid-phase protocol, modifying the methods of Longmire et al. (1997) and Rohland and Hofreiter (2007). Briefly, we incubated samples overnight with Longmire (BE) and MixPK buffers at 37°C, then centrifuged them for 2 min at 9,600 *g*, and transferred the supernatant of each sample to clean tubes. We carried out the process of DNA adsorption using 80 µL silica per sample and a high guanidine thiocyanate salt concentration buffer. We washed DNA adsorbed onto the silica with wash buffer. Finally, we loaded supernatant onto empty spin columns, we added 60 µL TE buffer, and centrifuged samples at 16,000 *g* for 1 min (see García et al. 2024 for further details). In the polymerase chain reaction (PCR) amplification,

we used the primer pairs 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) to amplify in 2 reactions a 178 base pair (bp) region of the mitochondrial cytochrome c oxidase (COI). Illumina sequencing primers were attached to these primers at their 5′ ends. We verified library size in 2% agarose gels and purified libraries using the Mag-Bind RXNPure Plus magnetic beads (Omega Biotek). Then, we quantified libraries using Qubit dsDNA HSAssay (Thermo Fisher Scientific) and pooled them equimolarly. Finally, we purified and sequenced the pooled library in a NovaSeqPE250 run (Illumina).

We used FastQC software (Andrews 2010) to check the quality of demultiplex raw files and detect the Illumina adaptors, which were trimmed using CUTADAPT (Martin 2011), and the paired reads were merged with FLASH2 (Magoč and Salzberg 2011). Filtering based on the length of the fragment, the number of mismatches in the primers (up to 2), and the quality (Phred quality score ≥20) was applied. Then, we dereplicated filtered sequences (-derep fulllength) using the VSEARCH bioinformatic tool (Rognes et al. 2016). We carried out de novo chimera detection using the UCHIME algorithm (Edgar et al. 2011) implemented in VSEARCH. Finally, sequences were clustered at a similarity threshold of 98% (–cluster fast, –centroidsoption) following Shutt et al. (2020).

We performed the taxonomic identification 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%. We used the Robeson et al. (2021) database for the taxonomic identification of the sequences. Unassigned operational taxonomic units (OTUs) and singletons (i.e., OTUs containing only one member sequence in the whole dataset) were removed. We checked taxonomic identification on a case-by-case basis and modified when necessary. This is because in some cases, automatic identification cannot differentiate between closely related species due to the small fragment of COI used, and may even sometimes identify species that are not present in the study area (likely because the specific sequence is not available in public archives). We also removed those OTUs occurring at a frequency of <0.1% in each sample to avoid cases of accidental and secondary consumption (Deagle et al. 2019).

Estimation of Ecosystem Services-Disservices Trade-off

For each bird species (n = 26; Supplementary Material Table 1), we calculated the weighted percentage of occurrence (wPOO; Equation 1) to estimate the contribution of each prey taxa to the diet using the equation:

$$\text{wPOO}_i = \frac{1}{S} \sum_{k=1}^{S} \frac{I_{i,k}}{\sum_{i=1}^{T} I_{i,k}}$$

(1)

where S is the number of fecal samples, T is the number of food items (taxa), and $I_{i,k}$ is an indicator function with values 1 when the food item i is present in sample k. wPOO indicates the proportion of times that taxon i is present in a sample. However, unlike other parameters (e.g., percentage of occurrence, POO) in its formulation it weights every sample equally, and hence, avoids the overrepresentation of samples with a high number of taxa (see Deagle et al. 2019).

We employed multifactorial classification, a novel approach for classifying prey taxa according to both an ecological and

an agronomic perspective. First, following an ecological approach, we classified arthropods (including parasitoids) as either phytophagous or mesopredatory and discarded other functional groups (i.e., animal parasite, aphidicolous, detritivorous, fungivorous, omnivorous, plant disease vector, pollinator, and zoophytophagous) from subsequent analyses (see also Ocampo-Ariza et al. 2023). In a second step, following an agronomic approach we classified (and selected) apple pests (i.e., phytophagous feeding on apple trees according to literature and online resources) and natural enemies (i.e., mesopredators preying on apple pests; see also Garfinkel et al. 2022). We considered a mesopredator as a natural enemy of apple pests only if (1) the interaction has been previously recorded (e.g., *Episyrphus balteatus* feeds on *D. plantaginea*); (2) the predator has been observed on apple trees and it is reasonable to assume that they forage on pests (e.g., generalist predators like *Araniella cucurbitina* can feed on *D. plantaginea*); or (3) a previous interaction between the pest and the predator has been recorded at the genus level (e.g., *Epistrophe* sp. feeds on *D. plantaginea*, so we assume *E. grossulariae* observed in orchards can also feed on this aphid). For parasitoids, as the parasitoid–host relationship is usually much more specific, we considered natural enemies to be only those with recorded interactions. We calculated the cumulative wPOO of the different categories (phytophagous: wPOOpt; mesopredators: wPOOpr; apple pests: wPOOap; and natural enemies: wPOOne) as the sum of the species wPOO belonging to each one.

For each bird species, we calculated 2 ES-ED trade-off estimators based on the ecological and agronomical prey categorization of their diets. As an ecological estimator, we calculated a *trophic position* parameter (modified from Levine 1980; Ishikawa et al. 2023; Equation 2).

$$TP_i = \frac{\text{wPOOpt}_i}{\text{wPOOpr}_i + \text{wPOOpt}_i} + \left(\frac{\text{wPOOpr}_i}{\text{wPOOpr}_i + \text{wPOOpt}_i} \times 2 \right)$$

(2)

The trophic position of bird species i (TP_i) is the sum of the relative frequency of wPOO of phytophagous and mesopredator species giving double weight to mesopredators. Thus, TP_i ranges between 1 (all preys are phytophagous) and 2 (all preys are mesopredators). A value below 1.5 indicates a higher phytophagous wPOO compared to mesopredators wPOO, while a value above 1.5 indicates the opposite.

As an agronomic estimator, we established the agronomic quality (Equation 3) as the ratio between the wPOO of prey cataloged as apple pests and that of natural enemies of the pests. We considered bird species that frequently preyed on pests but not on their natural enemies as having a higher agronomic quality.

$$AQ_i = \frac{\text{wPOOap}_i}{\text{wPOOne}_i}$$

(3)

A higher agronomic quality (AQ_i) value of bird species i implies that pests are overrepresented in the diet of this species compared to natural enemies. In addition, as a complementary agronomic index, we calculated the proportion of apple pest species (PP_i, Equation 4) present in the diet of each bird species (p_i) with respect to the total number of apple pest species recorded in the whole database (P).

$$PP_i = \frac{p_i}{P}$$

(4)

Bird Species' Potential Contribution to the Pest Control Service

We estimated the potential contribution (PC_i) of a given bird species to the assemblage pest control services (Equation 5) by multiplying its agronomic quality (AQ_i) by its abundance in the whole bird assemblage (A_i), weighted by the degree of insectivory of its diet (I_i).

$$PC_i = AQ_i (A_i \quad I_i)$$
(5)

We weighted abundance by degree of insectivory because our assemblage harbored species whose global diets could be dominated by food items other than invertebrates (e.g., fleshy fruits; García et al. 2024), and hence, an estimation based exclusively on abundance could overestimate the role of a species in the assemblage. The degree of insectivory of bird species (i.e., percentage of invertebrates present in diets with respect to other feeding resources such as fruits, seeds, etc.) was obtained from the Elton Traits Dataset (Wilman et al. 2014), but modifying the lowest category (0 in the Elton Traits Dataset, but 10 in the present case) because all 26 bird species recorded preyed on arthropods in our assemblage (based on our fecal samples). Before multiplication in Equation (5), we transformed the degree of insectivory into a proportion. This approach combines a quality component (agronomic quality) with a quantity component (abundance weighted by degree of insectivory), and it is equivalent to the effectiveness framework used to assess species contributions in other animal-driven ecosystem services, such as seed dispersal and pollination (González-Castro et al. 2015, Gómez et al. 2022).

Statistical Analyses

Drivers of ecological and agronomic roles of bird species as pest controllers

We sought to understand first the drivers of bird species' role in ecological terms, that is, to explain the reasons underpinning the differences between bird species in trophic position. For this, we first characterized birds using the following functional traits: body weight (g), beak length (mm), gape width (mm), Kipp's index, tarsus, and tail length (mm) (Supplementary Material Table 1). For all traits, we used the species average value of measurements obtained during mist-netting. Body weight relates to the magnitude of resource consumption of individuals and beak morphology to the food type and size that the species can handle. Kipp's index, a measure of wing pointiness, represents flight strength and ability to cross open habitats (González-Varo et al. 2023), and it is estimated from Kipp's distance divided by wing length. Finally, tarsus and tail lengths inform us about the foraging strategy of species (i.e., method, substrate, location) and their locomotion ability, such as flight maneuverability in vegetation (Luck et al. 2012, Pigot et al. 2020). Avian morphological traits were highly correlated with one another (Pearson correlation coefficient, $r = 0.82$ on average; range: 0.58–0.93). Thus, we performed a principal coordinates analysis (PCoA) by means of the *pcoa* package (Paradis and Schliep 2019) in R 4.2.1 (R Core Team 2022), and used the 2 first axes as synthetic trait variables. We employ PCoA in preference to other multivariate techniques, such as principal component analysis (PCA), because the resulting configuration allows for the optimal reflection of the original distances between points (Zuur et al. 2007). Subsequently, we evaluated how the trophic pos-

ition of birds depended on their morphological characteristics (i.e., species–specific projections on PCoA1 and PCoA2 axes) and their degree of insectivory using a Gaussian linear model (identity link function, i.e., the default for a Gaussian distribution which does not apply any transformation to the response variable).

Then, from an agronomic point of view, we evaluated why bird species differed in their ability to provide ecosystem services vs. disservices depending on their insectivore diet. First, we regressed the agronomic quality index of species (i.e., the ratio between apple pests and their natural enemies within their diets) against their trophic position and mean relative abundance across apple orchards (Gaussian linear model, identity link). Then, to evaluate the potential of birds to control different sets of apple pests, we modeled the proportion of pests present in the diet of bird species (vs. all apple pests) against their trophic position and relative abundance by means of a generalized linear model with a quasibinomial distribution (as overdispersion was detected) and logit link function.

For each response variable (trophic position, agronomic quality, and proportion of pest species), we fitted every possible model, from those with a single fixed effect to models that included all fixed variables and their double interactions. The model with the lowest AIC_c value was selected as the optimal model (Supplementary Material Table 2). In those instances where >2 models exhibited a difference of <2 AIC units with respect to the optimal model ($\Delta AIC_c < 2$), we estimated the parameters of the full average. Linear and generalized models were fitted using the base function *glm*. To perform model averaging we used *dredge*, *get.models*, and *avg.models* from the package *MuMIn* (Bartoń 2023). Prior to the fitting of the models, the numeric fixed variables were scaled (mean = 0, SD = 1) to make the magnitude of their effects comparable.

Characterizing patterns of pest control potential at the level of bird assemblage

After characterizing the individual role of bird species in the trade-off between ecosystem services and disservices, we sought to upscale from species to the whole bird assemblage found in apple orchards. Thus, to visualize the relative contribution of the different bird species to pest control services, we located species in a 2-dimensional (2D) landscape defined by a quality (agronomic quality index) and a quantity (bird abundance weighted by their degree of insectivory) component (Schupp et al. 2010). Quality × quantity landscapes enable graphic representation, through bird species position regarding projected isoclines of species effectiveness in terms of the potential contribution to pest control, accounting for both the quantity of pests they can consume and intraguild predation. In addition, the way bird species are arranged within the landscape provides information about the main drivers of interspecific differences (i.e., abundance vs. diet-driven). To construct this landscape, we used the function *effectiveness_plot* of the *effect.lndscp* package (Jordano and Rodriguez-Sanchez 2017). Once the landscape was created, to evaluate if those species able to consume more arthropods were also those with a greater potential to control pests, we calculated the proportion of variance of the potential contribution to pest control landscape explained by each component (quantity, quality) by means of function *calc.relimp* in the *relaimpo* package (Groemping and Lehrkamp 2023).
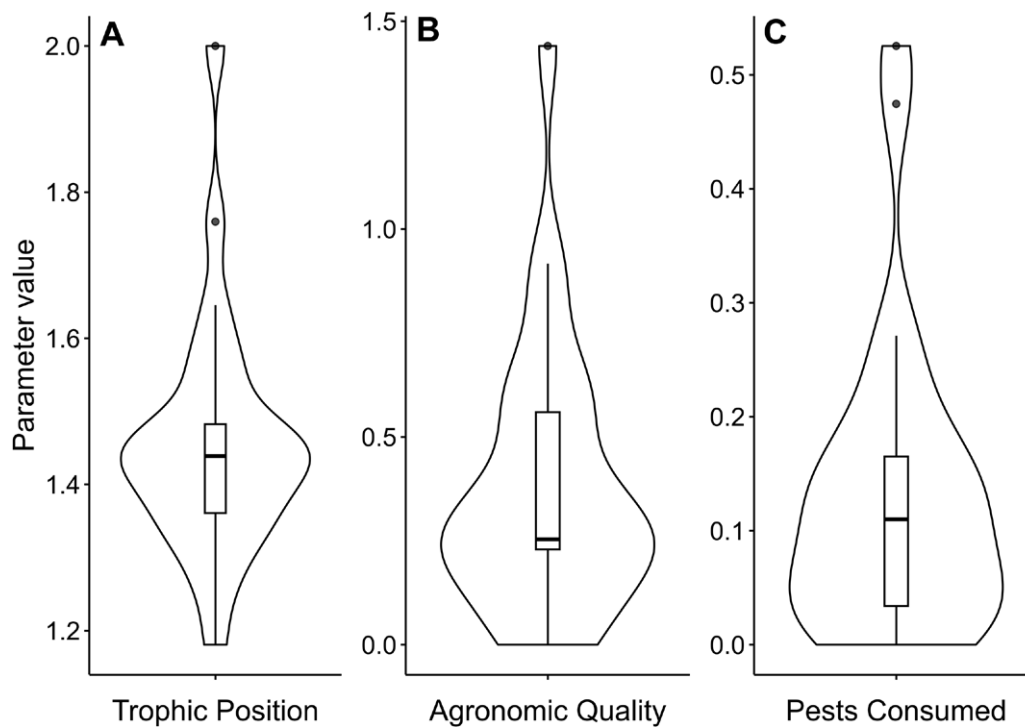
FIGURE 1. Violin plot and boxplot representing the distributions of the values per bird species of (**A**) trophic position, (**B**) agronomic quality, and (**C**) the proportion of apple pest species in the diet with respect to all the apple pest species recorded. In (**A**) values lower than 1.5 indicate that according to wPOO values bird species consume more phytophagous arthropods than mesopredators. In (**B**) values lower than 0.5 indicate that birds consume fewer pests than natural enemies.

RESULTS

General Overview of Bird Assemblage

A total of 1,070 individuals from 41 bird species were captured by mist-netting, from which 1,016 individual dropping samples were obtained across sites (23.1, 32.4, and 44.5% of samples in orchards 1 to 3, respectively). The proportion of samples obtained per month varied from 1.8%, in March 2020, to 15.0%, in December 2019. We recorded 910 individuals from 34 species, of which 41.4% were observed within the apple tree plantation and 58.6% in the woody hedgerows surrounding plantations. The bird assemblage was dominated by 3 species: *Erithacus rubecula* (European Robin), *Sylvia atricapilla* (Blackcap), and *Turdus merula* (Common Blackbird), with 15.7%, 13.6%, and 10.4% of relative abundance, respectively, while 10 species presented a relative abundance lower than 1%.

The first PCoA axis accounted for 82.16% of variance and represented increases in beak size (beak length and gape width) and weight (Supplementary Material Figure 2). The second PCoA axis explained 7.54% of the variance and was positively related to Kipp's index and negatively related to tarsus length, representing a gradient toward a more pointed wing and a shorter tarsus (Supplementary Material Figure 2).

Diet Composition

We performed molecular analyses on 550 individual fecal samples belonging to 26 bird species (average number of samples per species: 22.20 ± 4.35 SE). Metabarcoding analysis provided a global dataset of 3,786 OTUs assigned to 1,336 arthropod taxa. Of these OTUs, 56.2% were identified taxonomically to the species level, while the remaining ones were

assigned to the genus, family, or order levels (19.3%, 17.0%, and 7.4%, respectively). At the order level, Diptera (18.9% of the total wPOO), Hymenoptera (18.4%), Lepidoptera (17.8%), and Araneae (16.9%) were the dominant groups. In the ecological classification, 599 taxa were classified as phytophagous prey and 420 taxa as mesopredatory prey. These groups represent 35.3% and 28.3% of the total wPOO, respectively. Of these, following the agronomic approach, 59 taxa (4.8% of the total wPOO) were identified as apple pests, while 131 taxa (16.2% of the total wPOO) as their natural enemies (see Supplementary Material Table 5, in Supplementary Material Appendix B, for a list of prey taxa). Lepidoptera constituted 83.5% of apple pests wPOO, and Araneae accounted for 85.4% of natural enemies according to wPOO. Five of the 59 apple pests recorded in our diet database are considered of special concern in apple orchards in the study area (*A. pomorum*, *Aphis pomi*, *Aphis spiraecola*, *C. pomonella*, and *E. lanigerum*).

Estimation of Ecosystem Services-Disservices Trade-off

The trophic position of bird species tended to be close to 1.5 (mean ± SE = 1.45 ± 0.06; Figure 1A, Supplementary Material Table 3), indicating that the consumption of phytophagous arthropods and mesopredators was balanced. Nonetheless, there was high variability across species, with values ranging from 1.18 for *Carduelis carduelis* (European Goldfinch) to 2 for *Picus sharpei* (Iberian Green Woodpecker). Agronomic quality was generally low, with all species, except *Oriolus oriolus* (Eurasian Golden Oriole), presenting values below 1 (0.38 ± 0.06; Figure 1B; Supplementary Material Table 3), indicating that birds consumed more natural enemies than

TABLE 1. Results of generalized linear models (GLM) evaluating (**A**) the effects of ecological traits on the trophic position of the study bird species, (**B**) the effects of trophic position and bird species abundance on their agronomic quality, and (**C**) on the proportion of apple pests consumed. Significant effects are in bold ($P < 0.05$).

	Estimate	SE	t	P	R^2
(A) Trophic position (Gaussian [identity])					
(Intercept)	1.458	0.028	50.030	0.000	0.401
PCoA axis 1	−0.022	0.028	0.732	0.464	
Degree of insectivory	**0.086**	**0.030**	**2.767**	**0.006**	
PCoA axis 1 | Degree of insectivory	**−0.064**	**0.028**	**2.131**	**0.033**	
(B) Agronomic quality (Gaussian [identity])					
(Intercept)	0.298	0.037	7.583	0.000	0.300
Trophic position	**−0.112**	**0.039**	**2.707**	**0.007**	
Relative abundance	−0.054	0.039	1.309	0.190	
(C) Proportion of apple pests consumed (Quasibinomial [logit])					
(Intercept)	−2.209	0.320	−6.911	<0.001	0.156
Trophic position	−0.368	0.448	−0.820	0.421	
Relative abundance	−0.270	0.340	−0.793	0.437	
Trophic position | Relative abundance	−1.025	0.662	−1.547	0.136	

apple pests. Proportions of the total number of apple pest species present in bird diets were also low, with bird species consuming on average only 13% (±3.0 SE) of all the apple pests recorded across all fecal samples (Figure 1C; Supplementary Material Table 3).

Trophic position was positively affected by degree of insectivory, with this effect being modulated by the interaction with the first PCoA axis (Table 1; Figure 2A). Thus, insectivorous avian species fed more on mesopredatory arthropods, whereas bird species with an omnivorous diet (i.e., including other feeding resources, like fruits) consumed more phytophagous arthropods. Furthermore, these differences are more pronounced in larger species. The agronomic quality of birds depended on their trophic position (negative effect) while it was unaffected by the relative abundance of bird species (Table 1; Figure 2B). The proportion of apple pests in the diet was influenced neither by the trophic position nor the relative abundance of birds (Table 1).

Bird Species' Potential Contribution to Pest Control Services

The 2D landscape of potential contribution to pest control services (Figure 3A) clearly shows marked differences in relative position between the different bird species, depending on agronomic quality and quantitative component. Eleven out of the 26 species recorded (42%) were concentrated in the lower-left corner of the landscape, indicating that they scored low values for both quality and quantity components. Three species (*O. oriolus*, *Phylloscopus trochilus* [Willow Warbler], and *C. carduelis*) contributed poorly despite their high agronomic quality, due to their low abundance and low degree of insectivory. In contrast, other species with moderate values of quality and quantity attained relatively high values of contribution (e.g., *Turdus philomelos* [Song Thrush] and *Parus major* [Great Tit]). Finally, we found a disproportionate contribution of *E. rubecula*, *S. atricapilla*, and *T. merula* even though they showed a low agronomic quality (values <0.5). Such a pattern was driven by the dominance of these species in the bird assemblage (Figure 3A). Accordingly, the differences in the potential contribution across bird species were

mostly explained by the variability in the quantity component, as quantity accounted for 82% of the variance compared to the 3% accounted for by quality (Supplementary Material Table 4).

When species contributions were represented as cumulative values along an axis of bird species ranked by abundance, the potential contribution to pest control services showed a nonlinear, saturating pattern. The 6 most abundant species in our bird community dominated the contribution to the ES-ED trade-off (63% of the total contribution), whereas the contribution of rare species (<1% of relative abundance) was weaker (Figure 3B).

DISCUSSION

In this study we estimated, at the bird species level, the trade-off between ecosystem services and disservices in apple orchards resulting from the balance between bird predation on mesopredatory vs. phytophagous arthropods (trophic position) and on apple pests vs. natural enemies (agronomic quality). In addition, we evaluated how the ecological characteristics of birds affected the trade-off. We found that a bird species' trophic position responded positively to the degree of insectivory, and it represented an inverse surrogate of agronomic quality. These findings exemplify how to predict the net potential of bird species to impact on crop pests from insectivore diet. At the scale of the entire bird assemblage, we estimated the potential contribution of each species to pest control services, finding major differences that were mostly related to the abundance of each species. Our results highlight the importance of common bird species as effective pest control agents in agroecosystems, complementing the findings emerging from experimental (García et al. 2018, 2021) and interaction network studies (García et al. 2024).

Ecosystem Services-Disservices Trade-Off for Bird Species

The net effect of insectivorous birds on pest control has been demonstrated in experimental studies (Karp and Daily 2014, Maas et al. 2016, Ocampo-Ariza et al. 2023), establishing
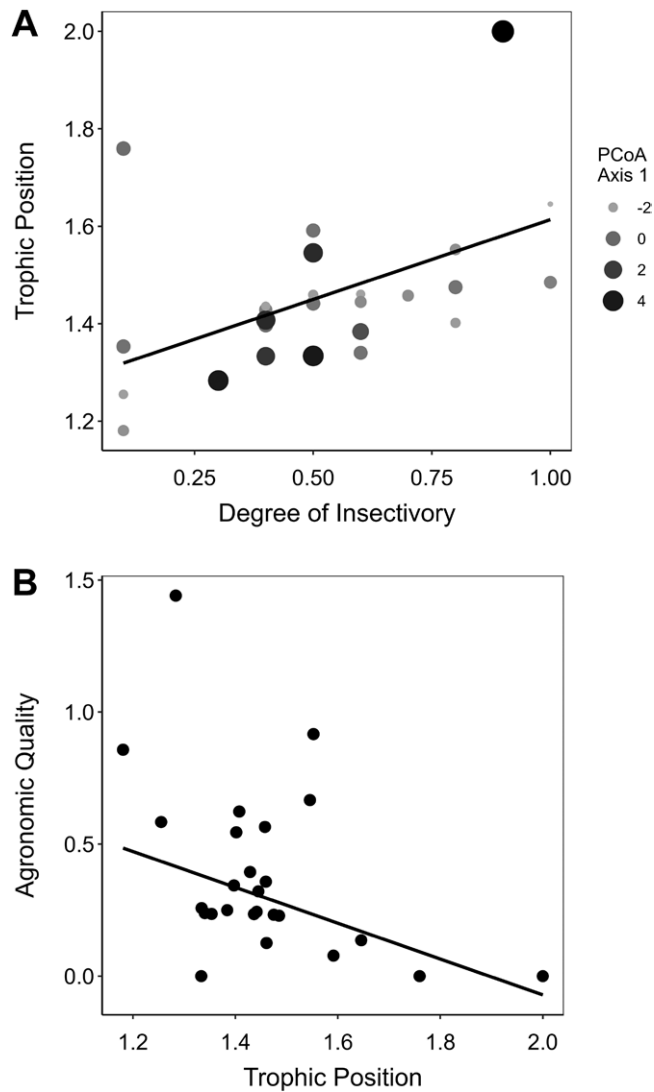
FIGURE 2. Relationships between (**A**) the trophic position and insectivore degree of the study bird species and (**B**) their agronomic quality and trophic position. Dots represent the values of different bird species. In (**A**), the size of the dots are adjusted by PCoA Axis 1 values. The line depicts the mean prediction of linear models (Gaussian distribution with identity link function).

FIGURE 3. Potential contribution of the study bird species to pest control services in apple orchards. (**A**) Landscape of species contribution based on their qualitative and quantitative component. The qualitative component was based on the agronomic quality of species estimated as the proportion of prey cataloged as apple pests vs. natural enemies. The quantitative component was estimated as the product of the abundance of species and their degree of insectivory. Isoclines depict the bidimensional variation of values of potential contribution emerging from the product of qualitative and quantitative components. (**B**) The cumulative contribution of bird species relative to their abundance ranks. Dots represent individual species, which are also indicated by their acronyms (for complete avian names see Supplementary Material Table 1).

them as an effective agent in this regard. These results (even in the case of the present study system; García et al. 2018) are used to recommend nonspecific management measures, such as preserving or increasing the presence of insectivorous birds in orchards (Smith et al. 2020, Mayne et al. 2023). However, this approach does not consider the specific roles of particular bird species, even when recognizing the existence of intraguild predation to infer these bird net effects (Karp and Daily 2014, Ocampo-Ariza et al. 2023). Our study focused on species roles and demonstrated that intraguild predation and the resulting ES-ED trade-off are prevalent but highly variable among insectivorous birds sharing local assemblages in the same agroecosystem. Thus, taking this variability into account is a first step toward explaining mechanistically (i.e., depending on bird assemblage composition) the overall effects of insectivorous birds on pest control in crops.

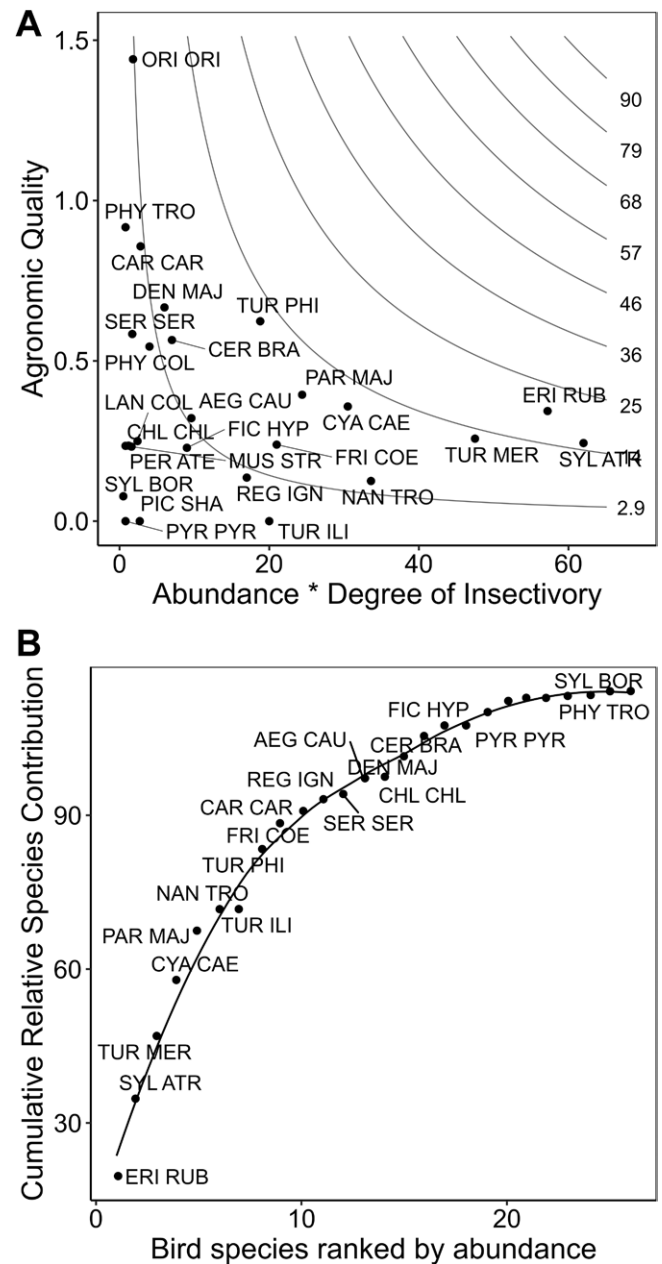From an ecological point of view, and according to the estimation of trophic position, our results indicated that most bird species showed a balanced diet between phytophagous and mesopredatory arthropods (Figure 1A, mean trophic position = 1.45). This was an unexpected result, given that lower trophic levels tend to show higher total biomass (Hatton et al. 2015), and that movement, escape and deterrence abilities are usually higher in mesopredators (e.g., Araneae and Apocrita)

than in phytophagous species (e.g., Aphididae, Lepidoptera, and Coccoidea) (Karp and Daily 2014).

Contrary to our expectations, bird traits did not affect trophic position, even though these traits have been proven to shape bird foraging environments (Carrascal et al. 1990, Moermond 1990). This lack of any effect on trophic position may derive from the observed gradient of variability covered by the studied bird species, rather than from the identity of traits considered. In this sense, the bird assemblage in the studied apple orchards could represent a narrow trait space, scarcely representing combinations of, for example, short tarsus and high Kipp's indices typical of aerial gleaners like swallows and martins (Hirundinidae), or long tarsus and long tails of ground gleaners, such as pipits (*Anthus* spp.). These bird taxa may have different diets compared to those of the typical vegetation gleaners sampled here, leading to different ES-ED trade-offs (Garcia et al. 2020). Nevertheless, we did find that bird species with a more insectivorous diet exerted a higher rate of intraguild predation among arthropods (Figure 2A). This effect was influenced by traits related to bird size (PCoA axis 1), indicating that the effect of an insectivore diet increased with the body size of the species. The adaptation of these stricter insectivores to prey on a wider range of arthropods could potentially increase predation on higher-level species, extending beyond the phytophagous species (Polis et al. 1989).

As expected, trophic position affected the agronomic quality of birds. Species with a higher position consumed fewer apple pests than natural enemies, suggesting a potential bias toward ecosystem disservices (Figure 2B). In this sense, the agronomic quality of avian species and the proportion of apple pests present in their diet was relatively low (Figure 1B, C). This result contrasts with the demonstrated global effects of birds in apple orchards, which indicate proven pest control even considering bird predation on natural enemies (García et al. 2018, 2021, Martínez-Sastre et al. 2020a). This incongruity may be due to the different scales at which birds feed on apple pests and natural enemies. The studied insectivorous bird species are generalist predators that frequently forage out of the orchards (e.g., woody hedgerows and adjacent forests) where natural enemies of apple pests may also occur (Bishop et al. 2023). In contrast, apple pests are typically crop-specialized species (Szentkirályi and Kozár 1991, Egas et al. 2004). The agronomic quality index established here measures the relative contribution of pests over natural enemies in bird diets, irrespective of whether they have been consumed inside or outside the apple orchard. Therefore, it may be biased toward low values of agronomic quality due to sampling effects. Our agronomic quality index allows us to infer the potential of bird species to provide services (vs. disservices) but it cannot be used to quantify the absolute effect of bird species within apple orchards. Within those limitations, it provides useful information about ecological characteristics of birds that can affect their pest controlling role in agroecosystems. We showed that birds that are more insectivorous and tend to have a higher trophic position are more likely to provide disservices than services. Thus, our approach highlights that the trophic position of insectivorous birds may represent a suitable biological indicator for predicting pest control potential with different crop types and in different regions, depending on the diet of the bird assemblages. Such a use of information on the diet of birds now seems feasible, given the technical advance of mass-sequencing methodologies (Mata et al. 2021).

The Potential Contribution of the Different Bird Species to Pest Control Services

Our results, along with previous studies (García et al. 2018, 2021, 2024), suggest that a limited number of common bird species appears to be sufficient to control pest populations in apple orchards in northern Spain, despite intraguild predation. The dominant role of a few abundant species in providing pest control services has also been observed in other agroecosystems (Jedlicka et al. 2011, Maas et al. 2015, Martínez-Salinas et al. 2016). In their meta-analysis, Philpott et al. (2009) emphasize the impact of common bird species on arthropod removal, proposing that sampling effects are key in understanding the importance of species richness as an indicator of pest control provision. To estimate the potential contribution of bird species to pest control services, we considered a metric related to their expected per capita contribution (agronomic quality) and a quantitative component associated with differences in abundance and degree of insectivory. Although bird species differed in quality (Figure 3A), their contribution patterns were mostly driven by the quantitative component (explaining 82% of variance). In other words, the most abundant taxa, which make up only 31% of the total number of studied species, account for more than 70% of the entire assemblage effect.

The cumulative pattern of species contributions (Figure 3B) also suggests that the net effect of species on pest control mostly depended on species abundances rather than other species attributes. That is, under a biodiversity-ecosystem functioning framework applied to trophic interactions (Letourneau et al. 2009) the present results suggest a preponderance of sampling (or dominance) effects over niche complementarity effects in pest control. After a certain threshold, the addition of new species only marginally increases the effect of the entire assemblage. This indicates that these species possess redundant functionality (Schleuning et al. 2015), which could positively impact the provision of ecosystem services in terms of enhanced resilience against species losses (Whelan et al. 2008, Liebman and Schulte 2015, Smith et al. 2022).

Concluding Remarks

Our results demonstrate how the trophic position of bird species, inferred from the insectivore diet, gives valuable information about their differential potential to provide ecosystem services of pest control. Contrary to the common perception among farmers (Martínez-Sastre et al. 2020b), our findings suggest that strict insectivores are not necessarily the most effective bird species to control apple pests. In fact, the trophic position was directly related to the degree of insectivory, indicating that highly insectivorous species showed an elevated rate of intraguild predation (e.g., on spiders). Such a pattern suggests a lower potential for ecosystem service provision of these species. Moreover, we found that bird relative abundance plays a dominant role in determining the potential contribution of the species in the ecosystem service. These results highlight the importance of common species with mixed diets (i.e., feeding on insects and other resources) for the maintenance of pest control as an ecosystem service (Gaston et al. 2018, García et al. 2024). We highly recommend conservation measures targeting these species (e.g., revised protection status), as well as farm management actions that foster their occurrence in apple orchards, i.e., preservation of hedgerows around orchards that provide alternative food resources, such as fleshy fruits, as well as nesting sites (García et al. 2024).

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

Ethics statement

This work has been carried out in accordance with the guidelines set out by the Spanish Government. The Government of the Principality of Asturias provided the necessary permits for scientific ringing (2019/014907, AUTO/2020/581).

Author contributions

Conceptualization: J.J.J.-A., T.M.-L., and D.G. Data curation: J.J.J.-A., J.C.I., M.M., and D.G. Formal analysis: J.J.J.-A. and T.M.-L. Investigation; J.J.J.-A., J.C.I., M.M., and D.G. Methodology: J.J.J.-A., J.C.I., M.M., and D.G. Visualization. J.J.J.-A. and T.M.-L. Writing: original draft. J.J.J.-A. and D.G. Writing: review & editing. J.J.J.-A., T.M.-L., J.C.I., M.M., and D.G. Funding acquisition: J.C.I., M.M., and D.G. Project administration: D.G.

Data availability

Analyses reported in this article can be reproduced using the data and R script provided by Jiménez-Albarral et al. (2025).

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