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Review

BIRD BIODIVERSITY AND PEST CONTROL IN AGROECOSYSTEMS: A MULTI-TROPHIC APPROACH

BIODIVERSIDAD DE AVES Y CONTROL DE PLAGAS EN AGROECOSISTEMAS: UNA APROXIMACIÓN MULTITRÓFICA

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SUMMARY.—Birds supply significant ecosystem services in agriculture, mostly by preying on pests across different agroecosystems and crop types. Nevertheless, the benefits of pest control may be set against avian attack on other natural enemies of pests (intraguild predation) or the crop damage caused by seed- and fruit-eating bird species that are themselves pests. In this review, we explore how pest control by birds is affected by avian assemblage size and the functional composition of bird communities, as well as by its environmental context. For this, we establish a conceptual framework of pest control integrating avian interspecific variability and trophic ecology. We evaluate the prevalence of positive, neutral or negative relationships between bird biodiversity and pest control, interpreting the mechanisms underlying these relationships. We also review the occurrence of trade-offs between pest control by birds and other ecological roles in agroecosystems. Finally, we assess how environmental factors shape pest control by birds, by accounting for the ecological processes that filter biodiversity and trophic interactions. Different syndromes of pest control by birds, based on pest body size and habitat physiognomy (i.e. openness) imposed by crop type, may be distinguished. We found generalised positive relationships between insectivorous bird biodiversity and pest control in croplands. These patterns emerge from either sampling effects (increased biodiversity involves the inclusion of dominant species), complementarity (inclusion of species complementary in their ecological niches) or facili-

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tation (inclusion of some species promoted by the presence of others), operating within local bird assemblages. Even though some studies evidence negative net effects of birds in agroecosystems, a positive or neutral overall balance is the most frequent outcome of the trade-off between avian pest control, intraguild predation and crop damage. Environmental gradients operating at different scales (from local plantations to the surrounding landscape) affect the diversity of birds as well as that of other natural enemies and pests, determining complex effects on species co-occurrence and interspecific interactions within crops. This context-dependence hampers the ability to predict pest control in real-world agroecosystems. Metabarcoding analyses of avian diet, combined with modelling of bird specific responses to environmental variation, may help to overcome these constraints and provide suitable tools for bird conservation and sustainable food production.—García, D., Illera, J.C., Jiménez-Albarral, J.J., Miñarro, M. & Morán-López, T. (2026). Bird biodiversity and pest control in agroecosystems: a multi-trophic approach. *Ardeola,* 73: 139-165.

Keywords: agriculture, avian ecosystem services and disservices, biodiversity-ecosystem functioning link, ecological trade-offs, landscape.

Resumen.—Las aves proporcionan importantes servicios ecosistémicos en la agricultura, principalmente a través del consumo de plagas en diferentes agroecosistemas y cultivos. No obstante, los beneficios del control de plagas pueden verse contrarrestados con la depredación de las aves sobre otros enemigos naturales de las plagas (depredación intragremial) o el daño a las cosechas causado por las aves granívoras y frugívoras (aves que actúan ellas mismas como plaga). En esta revisión, exploramos cómo el control de plagas ejercido por las aves depende del tamaño y la composición funcional de sus comunidades, así como de la heterogeneidad ambiental que las afecta. Para ello, establecemos un marco conceptual de control de plagas que integra la variabilidad interespecífica de las aves con su ecología trófica. Evaluamos la prevalencia de relaciones positivas, neutrales o negativas entre la biodiversidad de aves y el control de plagas, interpretando los mecanismos subyacentes a dichas relaciones. Revisamos la aparición de balances compensatorios entre el control de plagas y otros papeles ecológicos de las aves en los agroecosistemas. Finalmente, evaluamos cómo los factores ambientales modulan el control de plagas por aves teniendo en cuenta los procesos ecológicos que filtran la biodiversidad y las interacciones tróficas. Nuestra revisión muestra que se pueden distinguir distintos síndromes de control aviar de plagas, dependiendo del tamaño corporal de las plagas y de la fisionomía del hábitat (grado de apertura) que impone el tipo de cultivo. Encontramos relaciones positivas generalizadas entre la biodiversidad de aves insectívoras y el control de plagas en los cultivos. Estos patrones emergen a partir de efectos de muestreo (el incremento de biodiversidad implica la inclusión de especies dominantes), de complementariedad (inclusión de especies con nichos ecológicos complementarios), o de facilitación (inclusión de algunas especies promovida por la presencia de otras especies), que operan en los conjuntos locales de aves. Aunque algunos estudios evidencian efectos netos negativos de las aves en los agroecosistemas, un balance positivo o neutro es el resultado más frecuente del contraste entre control de plagas, depredación intragremial y daño de las aves plaga. Los gradientes ambientales a distintas escalas espaciales (desde el cultivo local al paisaje circundante) afectan a la biodiversidad de aves, de otros enemigos naturales y de plagas, determinando efectos complejos en la coocurrencia de especies y de sus interacciones interespecíficas en los cultivos. Esta dependencia del contexto dificulta la predicción del control de plagas en los agroecosistemas del mundo real. Los análisis de dieta de las aves basados en metabarcoding, junto con la modelización de sus respuestas específicas a la variación ambiental, pueden ayudar a superar estas limitaciones y proporcionar herramientas adecuadas para la conservación de aves y la producción sostenible de alimentos.—García, D., Illera, J.C., Jiménez-Albarral, J.J., Miñarro, M. y Morán-López, T. (2026). Biodiversidad de aves y control de plagas en agroecosistemas: una aproximación multitrófica. *Ardeola,* 73: 139-165.

Palabras clave: agricultura, balances compensatorios ecológicos, paisaje, servicios y diservicios ecosistémicos de aves, vínculo biodiversidad-funcionamiento ecosistémico.

INTRODUCTION

Agriculture is a major land use worldwide and agroecosystems now comprise the largest biome on Earth, occupying a third of the global ice-free land area (Ramankutty *et al*., 2008; Ramankutty *et al*., 2018). This makes agriculture probably the strongest environmental challenge faced by terrestrial bird biodiversity all over the world (e.g. Ormerod & Watkinson, 2000). The relationship between agriculture and bird biodiversity is, nevertheless, reciprocal and complex. Agriculture affects bird biodiversity both directly and indirectly, with frequent negative but sometimes positive outcomes. In this respect, habitat transformation derived from agricultural intensification is leading to avian decline worldwide (Inger *et al*., 2015; Rosenberg *et al*., 2019). The loss and fragmentation of natural habitats –such as forest and grasslands– associated with cropland expansion is driving such bird population declines and local extinctions both in tropical and temperate regions (Gregory *et al*., 2019; Oakley & Bicknell, 2022; Douglas *et al*., 2023; Rabbetts *et al*., 2023). Similar effects emerge from the habitat degradation imposed by intensive agricultural practices, through severe reductions in feeding and nesting resources for birds within the areas occupied by crops (Stanton *et al*., 2018). Importantly, pesticide use has been identified as a major threat to birds both through direct (i.e. toxicity) and indirect (i.e. food shortages) effects of insecticides, fungicides, rodenticides and herbicides (Stanton *et al*., 2018; Fernández-Vizcaíno *et al*., 2022; Rigal *et al*., 2023; Buij *et al*., 2025). Even so, some bird species may benefit from the habitat conditions created by extensive agriculture (e.g. birds of open habitats in heterogeneous farmland, Doxa *et al*., 2010; Traba & Morales, 2019) or from eventual resource inputs associated with intensive agriculture (Fox *et al*., 2016; Hemminger *et al*., 2022).

Birds, in turn, may influence the outcomes of agriculture in different ways, depending on their ecological roles. In this regard, avian predators are known to render positive agronomic services by controlling the populations of pest animals that damage crops (e.g. Díaz-Siefer *et al*., 2022; Monteagudo *et al*., 2023; Boldorini *et al*., 2024). For example, insectivorous birds can hamper aphid outbreaks in apple orchards, decreasing aphid damage on tree growing shoots by up to 70% (García *et al*., 2018). Such pest control comprises a top-down trophic cascade in which increased predation by birds on pests reduces plant damage, thereby increasing plant growth and/or reproduction (Whelan *et al*., 2016). Ultimately, pest control enhances crop yields and translates into direct economic benefit to farmers (Díaz-Siefer *et al*., 2022). For example, by reducing the attack of the Coffee Berry Borer *Hypothenemus hampei* in Jamaican and Costa Rican plantations, insectivorous birds contributed approximately US$310 per hectare per year in coffee yield (Johnson *et al*., 2010; Karp *et al*., 2013). These economic benefits of enhanced yield may be further increased when considering the reduction of costs in chemical pesticides (Johnson & Hackett, 2016).

Birds may benefit agriculture but may also cause a variety of damages to farmers (Ferrari *et al*., 2025). They cause crop losses when they themselves act as pests that consume seeds, fruits and plant buds (e.g. Gebhardt *et al*., 2011; Anderson *et al*., 2013; Sausse *et al*., 2021). Apart from the direct effects of plant-feeding birds, some indirect negative effects may emerge when birds prey on animals that are natural enemies of pests, limiting their impact (Martin *et al*., 2013). For example, nesting Tree Sparrows *Passer montanus* favoured aphid damage to cereal crops in Germany, due to their intense predation on hoverfly and ladybird larvae, the aphids' principal natural enemies (Grass *et al*., 2017). Such intraguild predation, and the concomitant pest release, may counterbalance the direct effect of insectivorous birds on crop-feeding arthropods and dilute pest control (Martin *et al*., 2013; Pejchar *et al*., 2018). Finally, bird faecal contamination of fresh crops, and the potential transmission of foodborne pathogens such as *Salmonella* sp. and *Escherichia coli*, frequently leads to partial crop discards and/or increased costs in management for food safety (Olimpi *et al*., 2019; Smith *et al*., 2020, 2021).

In sum, birds play a generalised role as pest control agents in agroecosystems, especially when insectivorous birds feed on arthropod pests (Díaz-Siefer *et al*., 2022; Monteagudo *et al*., 2023; Boldorini *et al*., 2024). Nevertheless, they may also cause direct and indirect negative impacts on agriculture that can overcome the benefits of pest control. Thus, the net effects of birds in agriculture need to be approached from the perspective of a trade-off between ecosystem services and disservices that ultimately determine changes in crop yield and rentability of farms (Peisley *et al*., 2016; Pejchar *et al*., 2018; Garcia *et al*., 2020). However, we are still far from understanding how and when avian pest control, i.e. pest control by birds, is counterbalanced by other ecological roles of birds in real-world agroecosystems. This is because the ultimate ecological mechanisms underpinning these trade-offs are intricate, due to the multiple and context-dependent interactions among birds, other natural enemies, pests and crop plants (Pejchar *et al.,* 2018; Monteagudo *et al.,* 2023; Boldoroni *et al.,* 2024).

Here, we present a biodiversity-based approach of bird effects on agriculture and review the recent literature to understand how avian pest control is ultimately affected by the size and composition of bird assemblages (i.e. the occurrence of different species with different functional roles regarding crops) and their environmental contingency (i.e. the factors that filter bird assemblages and affect bird activity). By the term ‘pest’, we consider herbivorous animal species able to directly or indirectly damage crop plants through consumption of any plant part, irrespective of their actual potential to produce economically significant losses to crops. Our specific goals are: 1) to establish a conceptual framework for pest control that integrates avian biodiversity and trophic ecology; 2) to evaluate the prevalence of positive, neutral or negative relationships between bird biodiversity components, such as bird abundance, species richness or functional diversity, and pest control in agroecosystems; 3) to address the potential mechanisms that underlie positive effects of avian biodiversity on pest control; 4) to review the occurrence of trade-offs between avian pest control and other ecological roles in agroecosystems; and 5) to assess how environmental factors shape avian pest control by accounting for the ecological processes that filter biodiversity and trophic interactions. We addressed objectives 1, 3 and 5 through a non-systematic, thematic-oriented survey of recent literature. Objectives 2 and 4 were explored through a systematic literature search of articles covering specific terms, and a qualitative vote-counting analysis of study cases provided by these articles, representing the presence/absence of different biodiversity relationships and trade-off effects (see Monteagudo *et al*., 2023, for a similar procedure). Patterns emerging from vote-counting analysis are discussed in relation to the potential inference limitations inherent to this type of methodology (e.g. non-independence of study cases from the same study, temporal changes in methodological quality, publication bias due to research scope or occurrence of significant effects).

A MULTI-TROPHIC APPROACH TO BIRD BIODIVERSITY EFFECTS IN AGROECOSYSTEMS

In principle, the potential of avian pest control in agricultural systems depends on the variety of species and trophic roles within the bird assemblages present in those systems (Philpott *et al*., 2009). Here we consider a view of bird biodiversity along two dimensions of interspecific variability (fig. 1; Duffy *et al*., 2007). Firstly, a vertical dimension represents bird species occurring across different levels of a trophic web based on crop plants. The upper level of this web is occupied by predatory birds that provide pest control by attacking major crop pests, such as insectivorous birds feeding on arthropods and raptors preying on granivorous vertebrates (A in fig. 1). These predatory species (notably insectivorous birds) may also exert

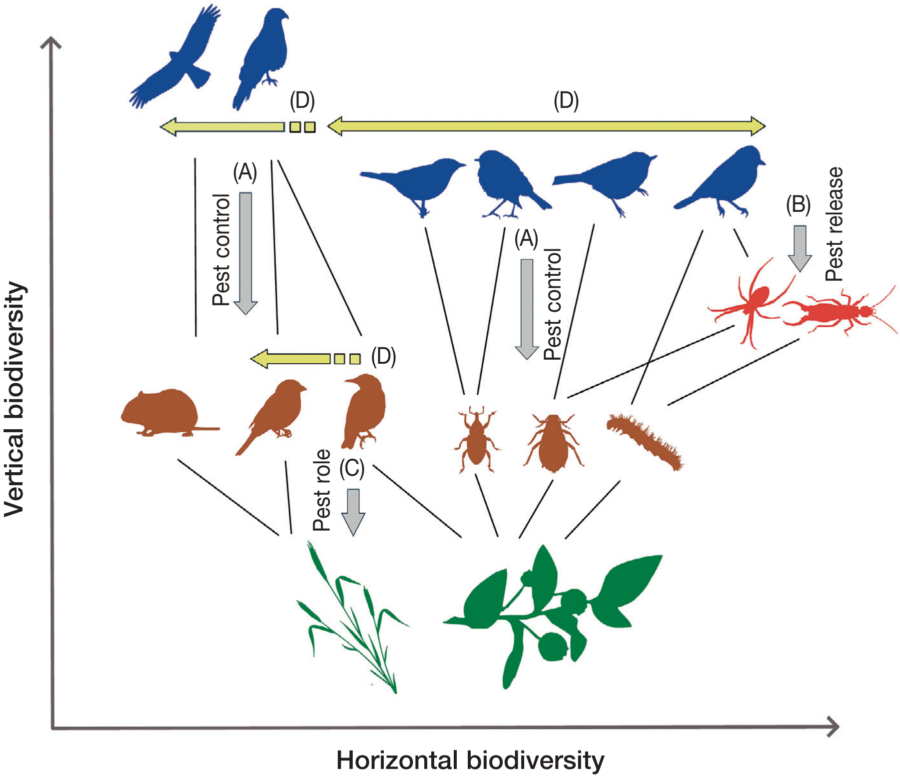

FIG. 1.—Representation of bird biodiversity along two dimensions accounting for trophic roles (vertical biodiversity, different silhouette colours represent different trophic levels) and taxonomic diversity (horizontal biodiversity, different species are represented). Vertical grey arrows highlight different roles of birds in agriculture depending on their position in the trophic web (A-C). Horizontal yellow arrows highlight variability in terms of the inclusion of different species within (e.g. insectivores) and across (e.g. insectivores and birds of prey, insectivores and granivores/frugivores) avian functional groups (D). *[Representación de la biodiversidad de aves a lo largo de dos dimensiones considerando los papeles tróficos (biodiversidad vertical, los diferentes colores de las siluetas indican distintos niveles tróficos) y diversidad taxonómica (biodiversidad horizontal, se representan distintas especies). Las flechas verticales grises resaltan diferentes papeles en la agricultura dependiendo de su posición en la red trófica (A-C). Las flechas horizontales amarillas resaltan la variabilidad en términos de inclusión de diferentes especies dentro (insectívoros) y a través (insectívoros y rapaces, insectívoros y granívoros/frugívoros) de los grupos funcionales de aves (D).]*

intraguild predation on mesopredatory animals (e.g. spiders, earwigs) that act as natural enemies, provoking an ecological release of pests (B in fig. 1). For these top predators, their net effect will thus depend on whether they mainly prey on pests or chiefly on natural enemies of pests. Along this vertical axis, other bird species may feed directly on crop plants, themselves acting as crop pests and occupying a lower trophic level (C in fig. 1). Secondly, a horizontal dimension accounts for interspecific variability within a single trophic level or functional group of birds (e.g. insectivores). This horizontal dimension, which is frequently estimated through taxonomic diversity (i.e. species richness), is highlighted as directly related to pest control (e.g. Martínez-Sastre *et al*., 2020; Yahya *et al*., 2024). Nevertheless, it could be expanded to incorporate larger assemblages of predatory bird species to characterise pest control globally (e.g. considering altogether raptors and insectivores; D in fig. 1). Moreover, it would enable accounting for roles that counterbalance pest-control, such as intraguild predation and crop plant consumption, even by the same bird species (D in fig. 1; Olimpi *et al*., 2022; Jiménez-Albarral *et al*., 2025).

This sort of bidimensional approach has been used to understand other ecosystem services driven by animal trophic activity (e.g.

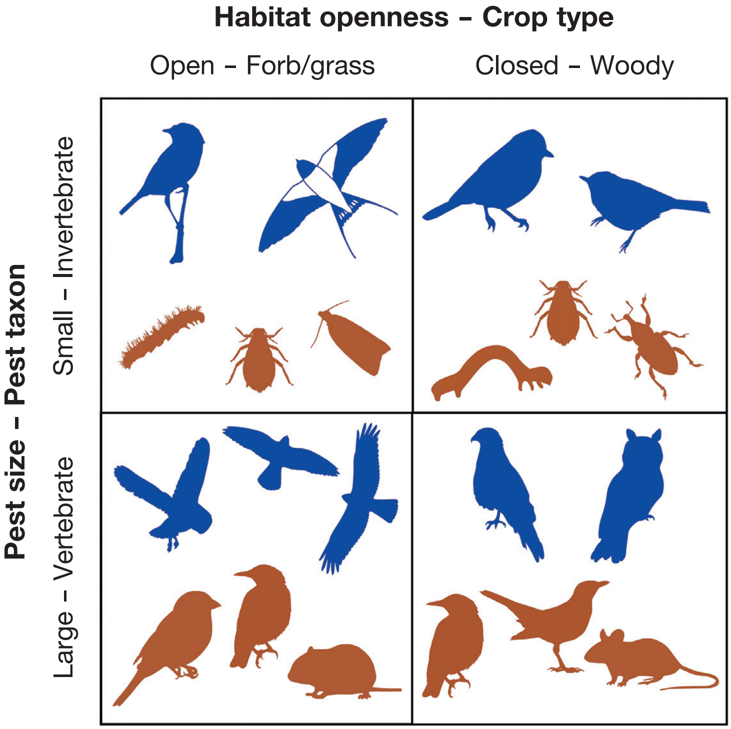

FIG. 2.—Representation of pest-control syndromes involving different predatory birds (in blue) and crop pest animals (in brown), according to crop type and pest size and taxon.
[Representación de síndromes de control de plagas considerando diferentes aves depredadoras (en azul) y animales plaga de cultivos (en marrón), dependiendo del tipo de cultivo y del tamaño y el taxón de la plaga.]

decomposition; Gessner *et al*., 2010), providing interesting findings such as the positive relationship between species richness across different trophic levels (i.e. a higher plant richness promotes greater herbivore richness which, in turn, fosters predator richness; Eisenhauer *et al*., 2019). However, this pattern has not yet been demonstrated with respect to avian pest control, where application of this framework has been scarce. So far, the role of trophic complexity for predicting pest control has been recognised by addressing how different species of insectivorous birds incorporate different proportions of pest arthropods and those that are natural enemies of pests in their diet (Garfinkel *et al*., 2022; Olimpi *et al*., 2022; Jiménez-Albarral *et al*., 2025).

BIRD BIODIVERSITY AND PEST CONTROL IN AGROECOSYSTEMS

A coarse-grained approach to bird biodiversity acknowledges that pest control in agroecosystems may emerge from a wide array of ecological combinations, depending on the functional types of birds, pests and crops (Díaz-Siefer *et al*., 2022). In particular, several pest-control syndromes may be proposed as a function of crop type (and the corresponding bird habitat physiognomy) and the size (and animal taxon) of the crop pest (fig. 2). Annual and herbaceous crops (cereals, maize, sunflower, vegetables, …) represent open habitats with vegetation of low vertical heterogeneity that favour the foraging of ground-, low vegetation- and air-dwelling birds. In these types of crops, different avian groups will provide control over pests with contrasting sizes. Small insectivorous birds such as stonechats, sparrows, and swallows will frequently prey on small invertebrates. For example, the Song Sparrow *Melospiza melodia* is an important pest consumer in the maize and soybean fields in Illinois, USA (Garnfinkel *et al*., 2020), and the Barn Swallow *Hirundo rustica* is a major predator of pests in Californian strawberry fields (Olimpi *et al*., 2020). In contrast, open-habitat raptors will control larger pest vertebrates, such as seed-eating rodents and birds. For instance, the Barn Owl *Tyto alba* preys intensely on crop-harmful mice and voles in the Central Valley in California (USA), especially in areas with a high proportion of non-perennial crops in the agricultural landscape (Kross *et al*., 2016a). Similar patterns have been observed for the Common Kestrel *Falco tinnunculus* in cereal and alfalfa crops in northern Spain (Montoya *et al*., 2021) and for Montagu's Harrier *Circus pygargus* in the Netherlands (Koks *et al*., 2007). In contrast to annual crops, woody perennial crops represent vertically complex habitats where pest control relies on shrubland and forest birds. There, again, different bird types prey on pests of different sizes. Small, tree-dwelling insectivores, such as warblers and tits, prey on insects in crops such as coffee, cacao, vineyard, and apple (e.g. Karp *et al*., 2013; Maas *et al*., 2015; Barbaro *et al*., 2017; García *et al*., 2018). Meanwhile raptors able to forage in dense-canopy habitats, such as kestrels, hawks and owls, may protect crops from fruit-eating birds and rodents (Lindell *et al*., 2018). For example, the Ural Owl *Strix uralensis* has been found to provide significant pest control of voles in apple orchards in Japan (Murano *et al*., 2019), whereas box nesting American Kestrels *Falco sparverius* protect cherry plantations against frugivorous birds (Shave *et al*., 2018).

Irrespective of the pest-control syndrome, a key issue is to understand the positive, causal relationship between bird biodiversity and pest control as an ecosystem function or service. In general, it is widely accepted that ecological communities hosting a larger variety of species provide ecosystem functions of greater magnitude and stability

(Loreau, 2010; van der Plaas, 2019). This positive relationship has been extended to ecosystem services (i.e. those ecosystem functions with direct or indirect effects on human well-being, Duncan *et al*., 2015) and has been tested in different animal groups (such as crop pollinating insects; Dainese *et al*., 2019; Loy & Brossi, 2022) and also specifically in birds (e.g. scavengers in carrion removal; Mateo-Tomás *et al*., 2017; frugivores in seed dispersal; García & Martínez, 2012). In the case of agricultural pest control, increases in service provision have been observed in areas with higher bird biodiversity. For example, bird attacks on plasticine models of caterpillars of an apple pest, the Codling Moth *Cydia pomonella*, has been found to increase with richness of forest insectivorous birds in apple orchards in northern Spain (fig. 3; Martínez-Sastre *et al*., 2020). Greater richness of insectivorous birds in crops has also been linked to decreased arthropod abundance on coffee plants (van Bael *et al*., 2008), and to decreased oil-palm damage from herbivorous pests (Yahya *et al*., 2024).

To check for the prevalence of biodiversity-ecosystem service links, we have reviewed studies evaluating how avian pest control may change at different levels of biodiversity in agroecosystems. In January 2025, we searched for publications in Web of Science (Clarivate) following the formulae “pest control AND bird AND crop” and

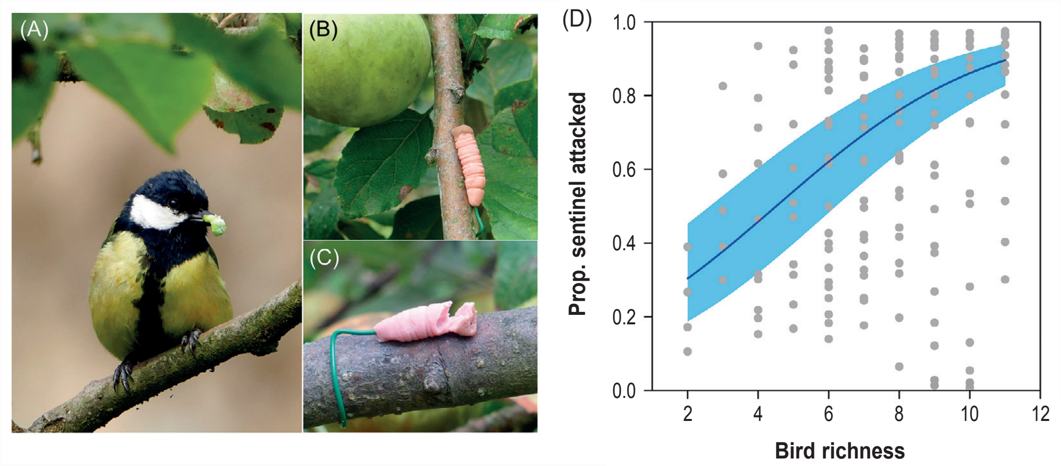

FIG. 3.—(A) A Great Tit *Parus major* feeding on a caterpillar captured in an apple tree. (B) Detail of sentinel plasticine model of Codling Moth *Cydia pomonella* caterpillar. (C) Signs of bird attack on a sentinel plasticine model. (D) The relationship between the proportion of sentinel models attacked by birds and bird species richness, for different apple plantations and dates in northern Spain (based on data from Martínez-Sastre *et al*., 2020). Confidence limits and fitted values of richness partial effects predicted by a binomial model are shown. Image credits: Marcos Miñarro (A), Daniel García (B, C).
[(A) Un Carbonero Común Parus major *alimentándose de una oruga capturada en un manzano. (B) Detalle de un modelo centinela hecho en plastilina de una oruga de Carpocapsa* Cydia pomonella. *(C) Signos de ataque de ave en un modelo centinela de plastilina. (D) Relación entre la proporción de modelos centinela atacados por aves y la riqueza de especies de aves en diferentes pomaradas y fechas en el norte de España (basado en datos de Martínez-Sastre* et al., *2020). Se muestran los límites de confianza y los valores ajustados de los efectos parciales de la riqueza predichos por un modelo binomial. Crédito de imágenes: Marcos Miñarro (A), Daniel García (B, C).]*

"pest control AND bird AND crop AND (abundance OR richness OR diversity)". We searched for additional suitable studies by checking reference lists in the initial publication search (ca. 60 publications) and surveyed new articles published from January to July 2025. From this article pool, we selected studies that explicitly tested the quantitative variation of pest control along gradients of bird biodiversity in croplands (i.e. across different sites or crop plantations). We discarded studies based on experiments of bird exclusion from crops (e.g. Maas *et al*., 2019) that account for birds exclusively in terms of presence/absence, as they do not represent actual quantitative gradients of bird biodiversity. Moreover, exclusion studies have largely been reviewed elsewhere (Maas *et al.,* 2019; Díaz-Siefer *et al*., 2022; Huang *et al*., 2023; Monteagudo *et al*., 2023; Boldorini *et al*., 2024), evidencing generalised decreases of pest control potential in the absence of birds (especially in cases of insectivorous birds preying on arthropod pests of woody crops). We also excluded studies promoting bird presence by manipulating the nest site or perch availability within croplands (e.g. nestboxes, perching poles), which have also found that increased bird presence increased pest control (e.g. Murano *et al*., 2018; García *et al*., 2021).

We found 18 articles published between 2008 and 2025 (Appendix 1) containing 40 cases (tests of response of pest control to biodiversity) that combined different parameters of bird biodiversity (total abundance, species richness, functional diversity) and functional outcomes of avian pest control (pest abundance, predation rate, plant damage, crop yield). Depending on the journal and research topic (Appendix 1), we classified the cases according to their scope under Biodiversity and Conservation (focused on bird biodiversity conservation in agroecosystems, 32.5% cases) or Agroecology (focused on the reciprocal interaction between birds and agriculture; 67.5% cases). The cases studied covered crops in tropical (57.5% of cases, N = 40) and temperate regions (42.5%), and a variety both of woody crops (apple, vineyard, olive, cacao, coffee, palm oil, walnut; 80.0%) and herbaceous crops (alfalfa, maize, cotton; 20.0%). Bird biodiversity was mostly estimated as total bird abundance or avian species richness (fig. 4A). Functional diversity was estimated in ca. 20% of cases and was quantified as functional richness (number of functional groups, e.g. Philpott *et al*., 2009), trait-based measures of functional evenness and dispersion (e.g. Martínez-Salinas *et al*., 2016) and, occasionally, phylogenetic diversity (e.g. Peña *et al*., 2023). The magnitude of pest control has been estimated in different ways (fig. 4B). In almost 40% cases, the rate of bird predation on pests was assessed by using indirect methods, such as the proportion of attacked sentinel pests (mostly caterpillar plasticine models, e.g. Barbaro *et al*., 2017, but also living lepidopteran larvae, e.g. Milligan *et al.,* 2016, or lepidopteran cocoons, e.g. Heath & Long, 2019). Other studies estimated the abundance of pests, frequently addressing the difference between crop plants from which birds were excluded and plants open to bird access across sites or plantations (e.g. van Bael *et al*., 2008). Pest control has been also addressed from agronomic estimates like crop plant damage (levels of defoliation, e.g. Yahya *et al*., 2024; or fruit damage, e.g. Martínez-Núñez *et al*., 2020) and, occasionally, as yield losses (e.g. Razak *et al*., 2019).

The vote-counting analysis indicated that, overall, studies evaluating the response of pest control magnitude to variable levels of bird biodiversity have found significant positive effects in almost 70% of cases (fig. 4C). Fewer than 30% of cases have indicated neutral relationships (i.e. non-significant statistical results in tests). Significant negative responses of pest control to increased bird biodiversity levels have been found in 5% of cases (fig. 4C). Overall, these results suggest that the positive effects of bird biodiversity on the magnitude of agricultural pest control are widespread across regions and crop types, particularly woody ones. These findings go beyond those of studies based on manipulating bird presence/absence through bird exclusion or addition experiments, as they account for continuous gradients of bird biodiversity and its different characterising components. Our findings are equivalent to that found in a meta-analysis on the effects of natural enemy biodiversity on the suppression of arthropod herbivores (with 70% of cases indicating herbivore suppression, Letourneau *et al*., 2009). Moreover, the preva-

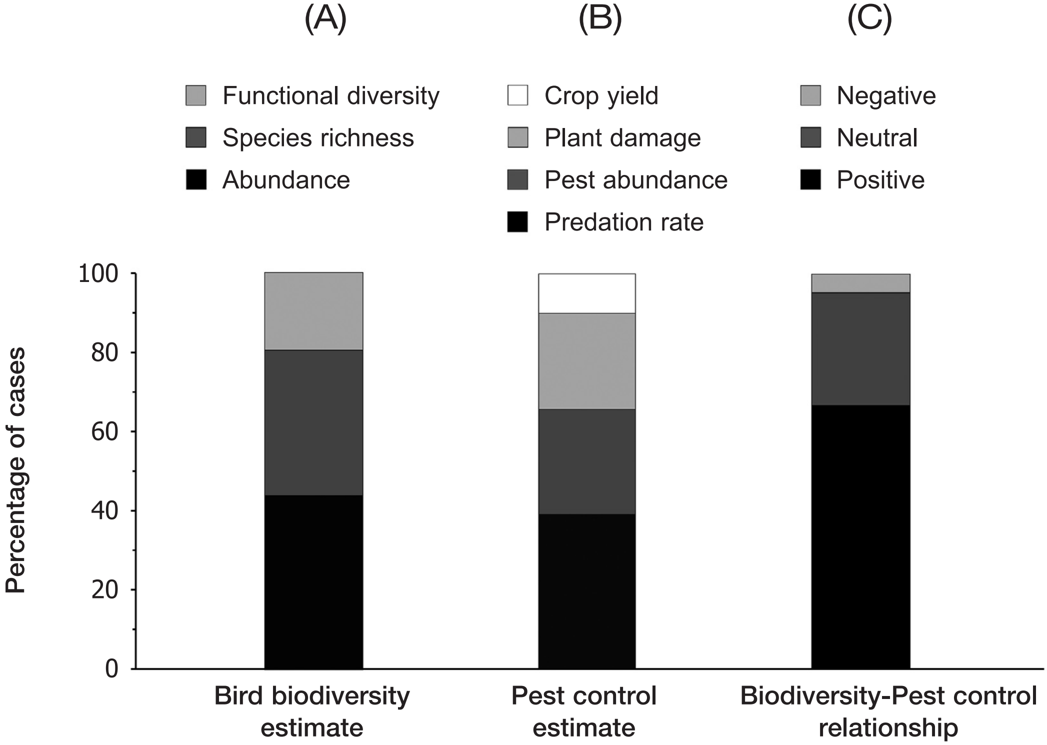

FIG. 4.—Results of vote-counting analysis on cases (N = 40, from 18 different studies) estimating the response of pest control magnitude to bird biodiversity in croplands. Columns represent the distribution of cases according to different parameters used to estimate (A) bird biodiversity, (B) pest control effects, and (C) the prevalence of positive, neutral or negative relationships between bird biodiversity and pest control magnitude (according to statistical tests modelling pest control response to bird biodiversity).

[Resultados de un análisis de conteo de votos en casos (N = 40, de 18 estudios diferentes) estimando la respuesta de la magnitud de control de plagas a la biodiversidad de aves en cultivos. Las columnas representan la distribución de casos de acuerdo con distintos parámetros usados para estimar (A) la biodiversidad aviar y (B) los efectos del control de plagas, así como (C) la prevalencia de relaciones positivas, neutras o negativas entre la biodiversidad de aves y la magnitud de control de plagas (de acuerdo con pruebas estadísticas modelando la respuesta del control de plagas frente a la biodiversidad aviar).]

lence of positive effects of biodiversity found here is higher than that estimated for other ecosystem services, including pollination of crop plants by animals (van der Plaas, 2019).

We consider the interpretation of these results to be barely affected by potential biases derived from vote-counting methodology. In this respect, the number of study cases per article was small (mean ± SE: 2.22 ± 0.25; min-max: 1-4) and the cases within each study frequently differed in the occurrence and nature of biodiversity effects (e.g. Kross *et al*., 2016; Barbaro *et al*., 2017; Razak *et al*., 2019; Peña *et al*., 2023). Also, studies covered a relatively short time span (years 2008-2025) and used direct-observation methodologies of comparable quality to assess pest occurrence, pest damage and pest control in crops (for example, no molecular assessment of bird diet was used for pest control estimation). Finally, we do not expect that there were publication biases associated with different research scopes, namely, positive biodiversity effects in Biodiversity and Conservation-oriented publications vs any sign effects in Agroecology-oriented publications. In fact, positive responses to bird biodiversity occurred in 74.1% of Agroecology cases (N = 27) but in 53.8% of Biodiversity and Conservation cases (N = 13). Moreover, only a third of articles represented studies having the causal relationship between avian biodiversity and pest control as a central question of research (Appendix 1), suggesting a low probability of bias towards positive significant effects for the whole study set.

MECHANISMS OF BIRD BIODIVERSITY-PEST CONTROL RELATIONSHIPS

The general theory on the positive link between biodiversity and ecosystem functioning provides a conceptual basis for understanding the ecological mechanisms underpinning avian biodiversity effects on pest control (Hooper *et al*., 2005). Namely, three non-excluding mechanisms have been signalled to explain why having a greater number of species in natural communities enhances ecosystem functions and services. Firstly, higher species richness frequently increases the probability of including species with a high functional performance, due to dominant abundance or higher resource acquisition ability (i.e. sampling effect; Hooper *et al*., 2005; Loreau, 2010). Secondly, greater richness may also entail the inclusion of functionally distinct species with complementary roles whose additive action leads to a greater magnitude of ecosystem functions (i.e. complementarity effect; Hooper *et al*., 2005; Loreau, 2010). Thirdly, greater richness in the community may promote interspecific facilitative interactions that foster shared contributions to ecosystem functions (i.e. facilitation effect; Hopper *et al*., 2005).

Sampling effects have frequently been suggested to explain positive effects of the biodiversity of natural enemies of crop pests (Letourneau *et al*., 2009; Crowder & Jabour, 2014; Jonsson *et al*., 2017). Dominant bird species have been found to drive the variability of total abundance within avian insectivore assemblages and the effects of such abundance on pest control (Maas *et al*., 2015; Kross *et al*., 2016b; Peña *et al*., 2023). For example, the very abundant Savanna Sparrow *Passerculus sandwichensis* and Red-winged Blackbird *Agelaius phoeniceus* provide the bulk of weevil control services in Californian alfalfa crops, shaping bird abundance trends and their functional effects (Kross *et al*., 2016b). This seems to be a generalised pattern, as bird assemblages in croplands normally show uneven abundance distributions, with common species contributing the most to pest predation (da Silva *et al*., 2024; García *et al*., 2024; Jiménez-Albarral *et al*., 2025). Moreover, the inclusion of dominant species frequently underpins the increases in bird richness that ultimately promote higher pest control, suggesting that richer assemblages provide stronger pest control just because they have a higher random probability of incorporating (i.e. "sampling") dominant species (Martínez-Sastre *et al.*, 2020).

Complementary effects driven by ecological niche partitioning between species have frequently been pointed out in studies of avian pest control. This is clearly suggested from the frequently found positive relationship between trait-based avian functional diversity and the magnitude of pest control (e.g. Martínez-Salinas *et al.*, 2016; Barbaro *et al.*, 2017). A wider dispersion of species in the functional space of a bird assemblage means the inclusion of species that are more differentiated in traits like body size, beak length and wing pointedness (Peña *et al.*, 2023). These traits are assumed to determine interspecific variability in food consumption rate, mobility and spatial behaviour, leading to distinct foraging syndromes or diet differences that result in complementary ecological roles (Moreno & Carrascal, 1993). For example, among the insectivorous birds visiting apple orchards (Peña *et al.*, 2023), differences in feeding substrate (e.g. ground, bark, branches, foliage) condition the access to different pest species and entail additive contributions to pest control. Indeed, bark-gleaning species, such as the Great Spotted Woodpecker *Dendrocopos major,* may easily access Codling Moth cocoons whereas foliage-gleaners, like Blue Tit *Cyanistes caeruleus*, frequently feed on aphid colonies or apple blossom weevils (García *et al.,* 2021, 2024).

Functional complementarity in pest control is now being explicitly addressed through avian dietary analyses based on DNA-metabarcoding techniques, which identify the arthropod prey species present in gut or faecal contents (e.g. Jedlicka *et al.*, 2017; Mata *et al.*, 2021). Metabarcoding assessment has its limitations for estimating prey consumption rates accurately and inferring net effects on pest population sizes (Cuff *et al.*, 2022). Nevertheless, it is suitable for estimating prey occurrence across different consumer species, from which to measure niche partitioning through approaches of dietary overlap (e.g. Zurdo *et al.*, 2023) and ecological interaction networks (Mata *et al.*, 2021). Namely, network modules represent non-random subsets of bird and pest species that interact more frequently among themselves than with other species. In other words, modules associate different bird species with different pest species, providing a measure of complementarity in avian pest control. For example, the bird-pest network in Spanish apple orchards, comprising 23 bird and 49 pest species, has been organised into six modules (fig. 5; García *et al.*, 2024).

Interspecific facilitation has frequently been assumed in bird assemblages, and mixed flocks of insectivorous birds have been documented in forest habitats worldwide (Sridhar *et al.*, 2009). Although often hampered in agricultural landscapes (e.g. Goodale *et al.*, 2013), flocking has also been described in agroforestry systems such as coffee and cacao (e.g. McDermott *et al.*, 2015). In particular, mixed flocking is frequently associated with improved feeding efficiency and better protection from predators (reviewed by Sridhar *et al.*, 2009). Thus, mixed flocks may be expected to increase pest control magnitude through the facilitative effects across species, at least in croplands where habitat features still favour flock formation. This hypothesis, however, has not yet been tested.

Even though neutral and negative relationships between pest control and biodiversity are less frequent, they have also been reported (Letourneau *et al.*, 2009). Neutral effects may be expected when bird species are functionally redundant (i.e. with equivalent and interchangeable roles; Zamora,

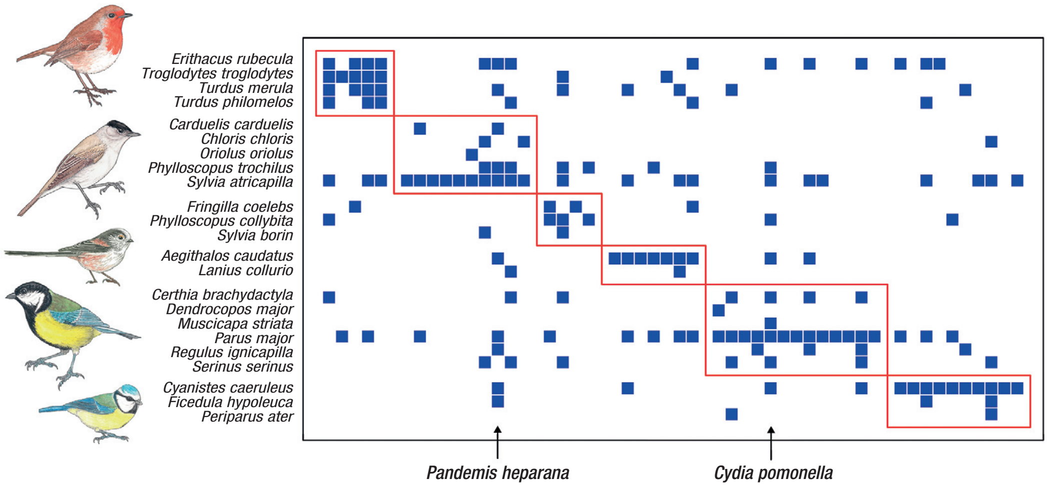

FIG. 5.—Modularity in interactions between bird species and different apple pests in apple orchards in northern Spain. Each blue square indicates a bird species-pest species interaction pair. Red rectangles indicate non-random modules of interactions (estimated by an LPAwb+ algorithm, Beckett, 2016). The main bird species in modules are represented, and two common apple pests are also indicated for exemplification. Note the occurrence of bird species from the same family (e.g. Paridae) in different modules. Modified from García *et al*. (2024). Artwork by Daniel García.
[Modularidad en las interacciones entre especies de aves y de plagas del manzano en pomaradas en el norte de España. Cada cuadrado azul indica un par de interacción interespecífica ave-plaga. Los rectángulos rojos indican módulos no-aleatorios de interacciones (estimados con el algoritmo LPAwb+, Beckett, 2016). Se representan las especies principales de aves en distintos módulos y se ejemplifican además dos plagas comunes del manzano. Nótese la aparición de especies de aves de la misma familia (e.g. Paridae) en distintos módulos. Modificado de García et al. *(2024). Ilustraciones de Daniel García.]*

2000). This is prone to occur when avian assemblages include numerous rare, small-contributing species that lead to an asymptotic pattern in the response of pest control to species richness (e.g. Jiménez-Albarral *et al*., 2025). Also, the occurrence of bird species performing intraguild predation (i.e. preying on other natural enemies and entailing a pest ecological release; Garcia *et al.,* 2020; Jiménez-Albarral *et al.,* 2025), may counterbalance the positive role of pest predators, leading finally to a null effect of avian biodiversity. Regarding the occasional negative effects of avian biodiversity on pest control or crop yield, they may be explained by the eventual dominance of bird assemblages by crop-harmful species, causing intense intraguild predation (Letourneau *et al.,* 2009) or even direct damage to plants (Razak *et al*., 2025). Finally, even when croplands host high levels of avian biodiversity and suffer intense pest attack, the link between bird biodiversity and pest control may be erased by endogenous and exogenous factors. For example, during endogenous pest outbreaks, avian predation may be insufficient to modulate pest populations (Kirk *et al*., 2016). Regarding exogenous factors, pesticide load may be the ultimate driver of pest abundance, decoupling pest population trends from avian predation (Martínez-Núñez *et al*., 2020).

TRADE-OFFS MEDIATED BY BIRD TROPHIC DIVERSITY

As described above, consideration of different avian trophic roles highlights how the effects of bird biodiversity, and the ability of birds to control pests, may be eventually counterbalanced by other ecological processes. The outcome of avian pest control in croplands will thus depend on how bird-provided ecosystem services (pest control) and disservices (intraguild predation, plant damage, food contamination) trade-off against each other (Pejchar *et al*., 2018; Gonthier *et al*., 2019). Beyond services/disservices directly associated with agriculture, other bird contributions such as birdwatcher recreation, seed dispersal and scavenging in adjacent habitats, as well as bird damage like noise or defecation nuisances, may be also considered when addressing the net effects of birds in agroecosystems (Whelan *et al*., 2015; Pejchar *et al*., 2018). Although the conceptual rationale of avian net effects in croplands is now well defined, empirical evidence on how bird biodiversity entails generalised positive, neutral, or negative overall balances is still lacking. This is partially due to the difficulty of finding a common currency to measure different bird ecosystem services and disservices in agriculture, but also to the different perspectives of approaching bird biodiversity from the viewpoints of ecology (e.g. biodiversity conservation) or agronomy (e.g. yield consequences; Pejchar *et al*., 2018). In this regard, Peisley *et al*. (2015) reviewed studies of costs and/or benefits of wild fauna in crop systems and found 70 bird-centred studies of which only 7.1% estimated both costs and benefits, in terms of monetary or yield values. Such low coverage led to inconclusive assessments of net effects.

To evaluate qualitatively the apparent patterns on how avian pest control trades-off with different disservices in croplands, we have searched for studies addressing simultaneously different agronomic effects of birds in croplands. We enlarged the literature search of the previous section "Bird biodiversity and pest control in agroecosystems", by adding the results of searches in Web of Science (Clarivate, January 2025), following the formulae "exclusion experiment AND bird AND crop" and "bird AND crop AND ecosystem services AND disservices". We selected studies that tested whether birds provide ecosystem services and disservices in the same agricultural setting. The trade-off between services and disservices could be measured explicitly (i.e. by quantifying pest control and disservices separately; e.g. Gonthier *et al*., 2019) and implicitly (i.e. by quantifying global outcomes, e.g. crop yield, that emerge from the trade-off between pest control and ecosystem disservices such as avian plant damage; e.g. Garfinkel *et al*., 2022). We found 48 studies published between 2008 and 2025 (Appendix 2) containing 80 cases (tests of evaluation of trade-offs). Most cases (92.5%) showed an Agroecological scope, and fewer than 10% had a Biodiversity and Conservation scope (Appendix 2). They combined different parameters of avian pest control (i.e. pest abundance, predation rate, etc.) and disservices (intraguild predation, predation on other beneficial arthropods, plant damage by birds, faecal contamination, etc.) assessed by different measurements (pest abundance, fruit damage rate, crop yield, etc.).

The cases of trade-off between avian ecosystem services and disservices were equally distributed between tropical regions (46.25% of cases, N = 80 cases) and temperate (53.75%) regions, and between woody (46.25%; e.g. apple, vineyard, olive, cacao, coffee, palm oil, walnut, macadamia) and herbaceous crops (53.75%; e.g. rice, soybean, sunflower, vegetables, strawberry, alfalfa, maize). Trade-offs were explicitly assessed in 37.50% of cases. Animal exclusion experiments in crops were used in most cases (78.75%; e.g. Martin *et al.*, 2013; Gonthier *et al.*, 2019; Linden *et al.*, 2019). Trade-offs involved the contrast between pest control and intraguild predation in more than 80% of cases (e.g. Maas *et al.*, 2013; Karp & Daily, 2014; Martin *et al.*, 2015; fig. 6A), and with seed or fruit damage on crop plants in 10% of cases (e.g. Kross *et al.*, 2012; Olimpi *et al.*, 2020; fig. 6A). Occasionally, disservices were estimated as bird predation on crop pollinators (e.g. Martínez-Salinas *et al.*, 2022) or as faecal contamination (e.g. Olimpi *et al.*, 2022). The net effect of trade-off was assessed in 75 cases through a variety of estimations, mostly of pest damage on plants, crop yield and of the abundance of pests and natural enemies (fig. 6B). A measure of multifunctionality synthesising plant damage by insects, plant damage by birds and faecal contamination was occasionally used (Olimpi *et al.*, 2020, 2022).

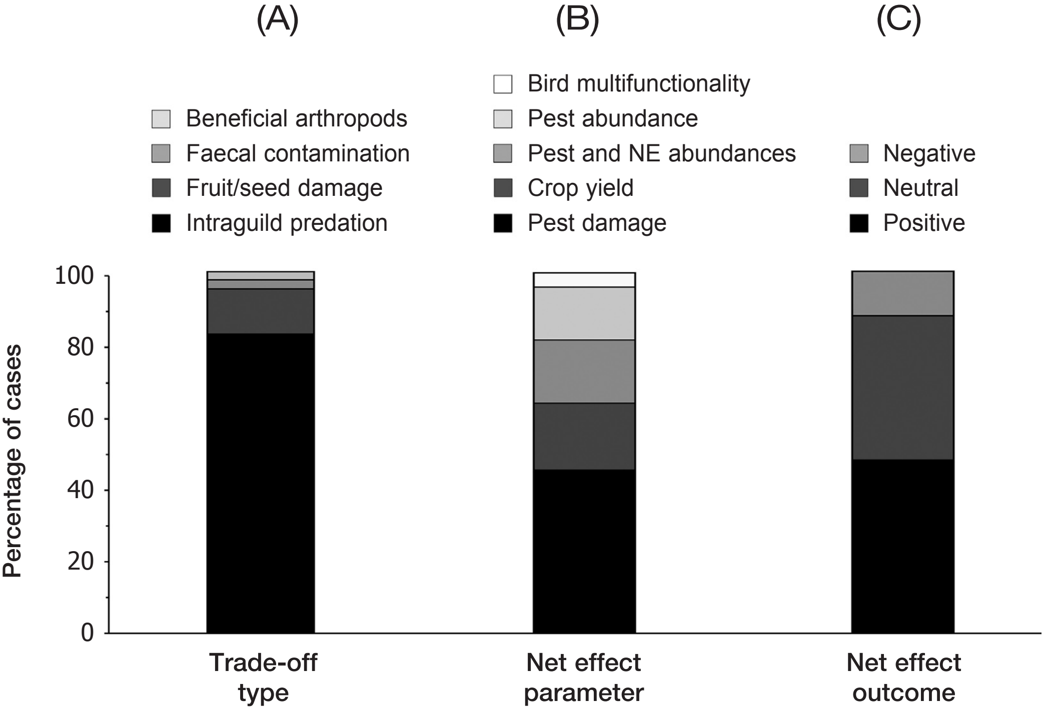

FIG. 6.—Results of vote-counting analysis on cases (N = 80 in A and 75 in B/C, from 48 different studies) estimating net effects of bird ecosystem services and disservices trade-offs in croplands. Columns represent the distribution of cases according to (A) the type of avian ecosystem disservice trading-off with pest control; (B) the parameter used for estimating the net effect of birds; and (C) the net outcome of the avian service-disservice trade-off.

[Resultados de un análisis de conteo de votos en casos (N = 80 en A y 75 in B/C, de 48 estudios diferentes) estimando los efectos netos del balance compensatorio entre servicios y diservicios ecosistémicos proporcionados por las aves en los cultivos. Las columnas representan la distribución de casos de acuerdo con (A) el tipo de diservicio ecosistémico que compensa con el control de plagas por aves; (B) el parámetro usado para estimar el efecto neto de las aves; y (C) el resultado neto del balance compensatorio entre servicios y diservicios aviares.]

The vote-counting analysis of the cases estimating the net effects of trade-offs between bird services and disservices showed that almost half of them suggested positive outcomes towards services (fig. 6C). For example, the benefits of avian pest control outweighed the detriments of intraguild predation in apple orchards of northern Spain, as suggested by the lower levels of plant damage by pests, together with the decreased abundances of pest and natural enemy arthropods, in bird-accessible compared to bird-excluded trees (García *et al*., 2018). In another example, in vineyards in New Zealand, avian pest control positively counterbalanced avian pest role, as shown by the decrease in grape damage after the introduction of New Zealand Falcons *Falco novaeseelandiae* that preyed on grape-eating birds (Kross *et al*., 2012). In 40% of cases, avian pest control services compensated for ecosystem disservices leading to neutral effects (fig. 6C). For instance, Gonthier *et al*. (2019) found that in California almost the same proportion of strawberry yield (3.2%) lost from direct bird consumption was gained (3.8%) due to the action of insectivorous birds preventing insect crop damage. The net effect of birds on crops was negative in only 12% of the cases studied (fig. 6C) and was due either to crop consumption rates by birds exceeding that of insect pests (Borkhataria *et al*., 2012) or to intense intraguild predation on natural enemies (Martin *et al*., 2013).

As judged from the variety of outcomes and underpinning mechanisms of net effects, the result of trade-offs between avian services and disservices seems highly context-dependent and difficult to predict from general rules (Garcia *et al.,* 2020). In any case, the type of crop seems to influence birds' net effects strongly. In crops with small, sweet fruits, such as blueberries, cherries and grapes the value of the production consumed by birds is likely to outweigh, or at least compensate for, the potential pest control benefits that birds could exert in these types of crops (Peisley *et al*., 2015; Garcia *et al.,* 2020). Moreover, as stated above in the test of bird biodiversity effects on pest control, here we would not expect any significant biases derived from the applied vote-counting methodology: the number of study cases per article was, on average, 1.66 (± 0.14 SE; min-max: 1-6); most studies showed methodologies of comparable quality (net effects were estimated from molecular tools in five cases, four of which showed positive effects, and one negative); very few cases corresponded to a Biodiversity and Conservation scope; and only 25% of articles represented studies explicitly designed to evaluate the net effect of trade-offs between avian ecosystem services and disservices (Appendix 2).

ENVIRONMENTAL DRIVERS OF BIRD BIODIVERSITY AND PEST CONTROL

Bird biodiversity has been found to vary substantially both across different types of crops (e.g. arable vs forage, Wilson *et al.,* 2017; tree crops, Luck *et al*., 2015) and among plantations of the same crop type (e.g. apple orchards, García *et al*., 2018; olive orchards, García-Navas *et al*., 2025). These varied environmental settings and landscape contexts entail differential filtering effects on bird biodiversity and may therefore affect the magnitude of avian pest control in croplands (e.g. Heath & Long, 2019; Mayne *et al*., 2023). Understanding the relationships between the environmental gradients associated with agriculture and the bird pest control outcomes is, thus, a prerequisite for improving avian ecosystem services through crop and habitat management (Tscharntke *et al*., 2016; Martin *et al*., 2019). In this regard, we need an integrative framework to predict how ecological processes shape the biodiversity of birds and their prey, as well as their trophic interactions, and how these processes are affected by the heterogeneity of agricultural habitats (fig. 7, Boesing *et al*., 2017; Pejchar *et al*., 2018).

The magnitude of avian pest control, and its trade-off with crop damage or intraguild predation, depends on the structure and functioning of trophic interactions between birds, arthropod pests, arthropod enemies of pests and crop plants (fig. 7). These ecological interactions depend on a plethora of proximate mechanisms determining bird ability to detect and handle arthropods as prey, such as phenological co-occurrence (e.g. bird migration, van Bael *et al*., 2008), sensorial ability (e.g. detection of plant volatiles associated with pest attack; Amo *et al*., 2016) and behavioural or morphological matching (e.g. foliage-gleaning behavior; Luck *et al*.,

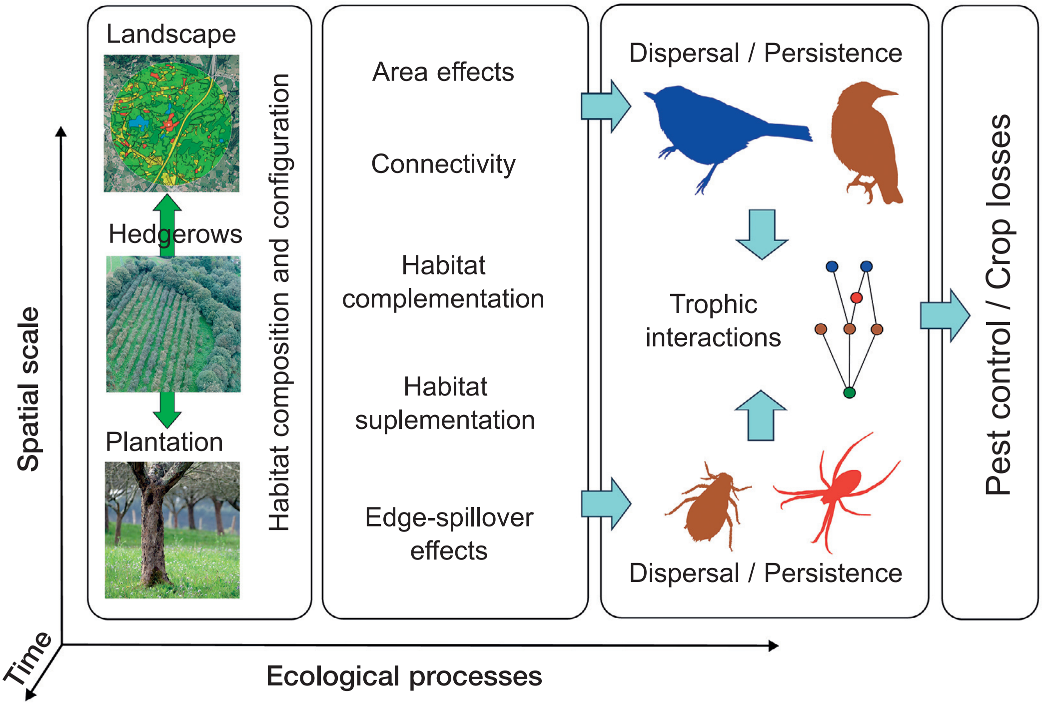

FIG. 7.—Integrative view of the environmental drivers of bird and arthropod biodiversity in croplands and the trophic interactions that shape pest control and/or crop losses. Different ecological processes at different spatial scales (from local plantation to landscape) affect the dispersal and persistence of avian and arthropod species and hence the trophic interactions of co-occurring species. Pale-blue arrows indicate causal or concatenated effects. The green bidirectional arrow highlights how plantation and landscape features may interact to affect bird and arthropod biodiversity.
[Visión integradora de los condicionantes ambientales de la biodiversidad de aves y artrópodos en los cultivos y de las interacciones tróficas que configuran el control de plagas y/o las pérdidas de cosecha. Diferentes procesos ecológicos a distintas escalas espaciales (desde la plantación local al paisaje) afectan a la dispersión y la persistencia de las especies de aves y artrópodos y, por tanto, a las interacciones tróficas de las especies concurrentes. Las flechas azules pálido indican efectos causales o concatenados. La flecha verde bidireccional resalta cómo las características de las plantaciones locales y del paisaje pueden interactuar para afectar la biodiversidad de aves y artrópodos.]

2012). Ultimately, bird-arthropod interactions are triggered by the occurrence of the different species within crops, resulting from processes of animal dispersal into crop patches and population persistence within them. Both ecological processes are modulated by different compositional and configurational gradients of habitats and landscapes that operate at different spatial scales, from the local scale of plantations to the large-scale surrounding landscape, and the intermediate scale of crop-adjacent hedgerows (fig. 7).

The multi-scaled gradients of habitat composition and configuration may involve different, non-exclusive effects on animal biodiversity. Firstly, area effects may emerge from the joint influence of the size of plantations (bird richness frequently being lower on larger farms, as crops may represent a less suitable habitat than surrounding seminatural patches, e.g. Belfrage *et al*., 2005) and the cover of seminatural habitats in the landscape (with bird richness in crops being proportional to, for example, surrounding forest cover, e.g. Boesing *et al*., 2018). Secondly, habitat connectivity, i.e. the spatial configuration of habitat elements promoting bird movement and occupation across the cropland space, may also matter not only at the landscape scale (Mühlner *et al*., 2010) but also at the plantation scale (e.g. greater apple tree cover within orchards facilitates insectivorous bird movement and occurrence; García *et al*., 2018). Thirdly, how different habitats are combined and compose the landscape around cropland is also a strong determinant of bird and pest biodiversity, through habitat complementation (how different habitat patches provide distinct complementary resources for animal species) and supplementation (how different patches, including croplands, supplement a given essential resource, such as nesting sites for insectivorous birds; García *et al*., 2021). The often-positive relationship between landscape heterogeneity –a measure of how landscapes represent a mosaic of different habitat patches around croplands– and bird richness is probably underpinned by such complementation/supplementation effects (Haslem & Bennet, 2008; Redlich *et al*., 2018). Moreover, local agricultural management frequently conditions the suitability of cropland as a habitat for birds, and hence its complementarity to seminatural habitats. For example, organic farming has frequently been associated with greater bird abundance and richness, when compared to conventional management (e.g. Belfrage *et al*., 2005; Katayama, 2016). Finally, edge effects are also relevant, reflecting the intensity of biodiversity spillover between croplands and adjacent semi-natural patches (Blitzer *et al*., 2012). These edge effects are frequently revealed by positive relationships between avian abundance and richness and the degree of adjacency (e.g. edge length) between crops and seminatural hedgerows (Heath *et al*., 2017; Wilson *et al*., 2017).

Plantation conditions derived from agricultural intensification deserve special attention as drivers of bird and arthropod biodiversity. In this sense, chemical inputs like insecticides produce both direct and indirect negative effects on the populations of both birds and arthropod natural enemies (Moreau *et al*., 2022; Schmidt-Jeffris, 2023). Richness losses and homogenisation in bird and natural enemy assemblages are also frequently associated with the use of herbicides and their impact on weed and ground herb covers (Chiron *et al*., 2014; Rey *et al*., 2019). Similar biodiversity modifications have been found in response to changes in the structural features of plantations, such as planting patterns based on higher densities of smaller trees (e.g. Morgado *et al*., 2022). Importantly, the effects of plantation-level intensification may depend on landscape-scale characteristics (fig. 7). Specifically, the reduction of intensification levels for promoting bird and arthropod biodiversity seems to be effective only in plantations surrounded by landscapes of intermediate complexity and seminatural habitat cover (e.g. Concepción *et al*., 2008; Rey *et al*., 2019; Hertzog *et al*., 2023; but see Castro-Caro *et al*., 2014). This intensification-landscape interaction is explained by the fact that no biodiversity spillover from seminatural habitats to plantations is expected when habitat cover is very low (due to scarcity of sources of colonisers) and, conversely, intense spillover, that is able to compensate biodiversity losses within plantations quickly, is expected in complex landscapes (*intermediate landscape hypothesis*; Concepción *et al*., 2008, 2012).

The modulating effects of environmental gradients on avian biodiversity frequently cascade into changes in pest control within croplands. Landscape-scale availability of seminatural habitats around crops enhances bird-mediated pest control in coffee plantations (Karp *et al.,* 2013), apple orchards (Peña *et al*., 2023), strawberry fields (Garcia *et al*., 2023), and vineyards (Koranyi *et al*., 2025). Effects of local crop management on bird abundance and the concomitant pest control have also been found (e.g. intensive vs extensive management in olive groves; Martínez-Núñez *et al*., 2020; but see Díaz-Siefer *et al*., 2022, for a meta-analytical comparison between organic and conventional farms). Nevertheless, the differential environmental responses of predatory birds, other natural enemies, and crop pests, or even of birds with different agronomic roles (natural enemy, intraguild predator, pest), may ultimately screen off the imprint of environmental gradients on pest control (Karp *et al*., 2018; Pejchar *et al*., 2018). For example, in cabbage crops in South Korea, intense predation by birds on flying insects, which are main natural enemies of Lepidopteran pests, led to greater pest release in crops in complex than in simple landscapes (Martin *et al.,* 2013).

Net effects of birds may also be affected by environmental gradients, depending on spatial variation in the relative balance between avian ecosystem services (pest control) and disservices (crop damage, intraguild predation). For example, in Californian strawberry farms, bird net effects depend on edge proximity and seminatural habitat cover, with negative outcomes seen close to farm edges and in farms with less seminatural habitat in their surroundings (Olimpi *et al*., 2020). Also, in diversified farms in the western USA, ecosystem disservices (crop damage, faecal contamination, bird nuisance and disapproval) and some cultural service (iconic value) decreased with increasing seminatural habitat cover, whereas no habitat effect was observed on avian pest control, recreational appreciation or conservation value (Smith *et al*., 2022).

CONCLUDING REMARKS AND FUTURE DIRECTIONS FOR RESEARCH

In this review, we synthesise what we have learnt on how avian biodiversity affects agricultural pest control at different levels. A coarse-grained view of avian biodiversity first enables establishing different avian pest-control syndromes based on pest body size and the habitat physiognomy (openness) imposed by the crop type. Focusing on bird assemblages sharing a similar trophic habit, we have found a frequent pattern of positive relationship between bird biodiversity and pest control in croplands, through different components such as total bird abundance, species richness and trait-based functional diversity. Thus, our findings expand on previous reviews based on avian exclusion experiments, which use a simplified approach to avian biodiversity (Díaz-Siefer *et al*., 2022; Monteagudo *et al*., 2023). Nevertheless, the general pattern presented here emerged from a relatively small number of studies mostly focused on woody crops and insectivorous bird assemblages. Thus, further metanalytical assessment, based on a larger number of studies covering wider variability in terms of crop types and bird functional guilds, would be required to strengthen the validity of our inference as well as to explicitly quantify publication biases from different sources (Díaz-Siefer *et al.,* 2022; Monteagudo *et al*., 2023).

As in other cases of biodiversity-ecosystem functioning links, richer bird assemblages provided stronger pest control due to the inclusion of dominant species (sampling effect), the gathering of species that are complementary in their functional niches, or even the incorporation of species that facilitate one another. Nevertheless, a fine-grained perspective of avian biodiversity acknowledges a variety of trophic roles with potentially negative agronomic effects. These include pest release due to intraguild predation on natural enemy insects, and direct plant damage via fruit and seed consumption, which may ultimately override the benefits of pest control. Our literature survey suggested that negative net effects of birds do occur in agroecosystems, although most of the studies report positive or neutral outcomes for the trade-off between avian ecosystem services and disservices.

Explicit evaluation of biological variability in bird assemblages, accounting for the different avian trophic roles, is therefore necessary for re-evaluating the strength and shape of the relationship between bird biodiversity and pest control in croplands. This may be achieved by characterising the agronomic contribution of individual species through, for example, diet analyses that quantify the consumption of pests, natural enemies and crop plants (e.g. Olimpi *et al*., 2020; Jiménez-Albarral *et al*., 2025). Estimating individual species values may enable the calculation of agronomic functional diversity for local bird assemblages, from which bird biodiversity-net effect relationships may be assessed.

Finally, the heterogeneity of patterns, and the complexity of ecological processes linking the environmental settings of crops and pest control, hamper our ability to predict pest control at both the local scale of plantations and the large scale of regional landscapes. Assemblage models accounting for the differential species responses to environmental variables, such as the Hierarchical Model of Species Communities (HMSC; Ovaskainen *et al*., 2017), offer suitable tools to overcome this constraint. These models can explain bird species responses based not only on traits but also on agronomic functional characteristics (as depicted above) and may finally be used to predict net avian effects, once validated with field measures of bird functional outcomes such as pest population sizes and crop yields. Predicting pest control as a trade-off between avian ecosystem services and disservices, while considering environmental gradients and bird biodiversity, would enable us to establish efficient crop management and land use strategies aimed at optimising food production alongside bird conservation in agricultural landscapes.

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curation: all authors equal; Formal analysis: DG; Funding acquisition: DG (equal), TM-L (equal); Investigation: DG (lead), JCI (supporting), JJJ-A (supporting), MM (supporting), TM-L (supporting); Writing – original draft: DG; Writing – review & editing: all authors equal.

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Appendix 1. List of references of studies used for evaluating the prevalence of relationships between bird biodiversity and pest control in agroecosystems.
[Listado de referencias de estudios utilizados para evaluar la prevalencia de las relaciones entre la biodiversidad aviar y el control de plagas en agroecosistemas.]

Appendix 2. List of references of studies used for evaluating the net effects of trade-off between avian ecosystem services (pest control) and disservices in agroecosystems.
[Listado de referencias de estudios utilizados para evaluar los efectos netos de la compensación entre los servicios ecosistémicos aviares (control de plagas) y los perjuicios en los agroecosistemas.]

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