Journal of Applied Ecology

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Article type : Research Article

Handling Editor - Lorenzo Marini

Enhancing ecosystem services in apple orchards: nest boxes increase pest control by insectivorous birds

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Abstract

1. Ecological intensification in croplands aims to enhance biodiversity-based ecosystem services, helping to increase yield while reducing agricultural environmental impacts. Identifying ecological intensification tools of wide applicability and easily implemented by farmers is, therefore, an imperative. Here, we verify the efficiency of provisioning artificial nest boxes for insectivorous birds to reinforce pest biological control in apple orchards.

2. The study was conducted in 24 cider-apple orchards in Asturias (NW Spain) over three years. We compared the effect of insectivorous birds between orchards with and without nest boxes occupied by different bird species, through insectivory estimates based on attack on a sentinel pest and measurements of arthropod abundance in apple trees. We also identified preys that birds of different species captured to feed nestlings.

3. Bird occupancy of nest boxes was widespread, ranging 25.0-33.3% each year. Great tit was the dominant species, followed by blue tit and, occasionally, common redstart.

4. Predation pressure on apple pests increased in orchards with nest boxes, as judged by the increased proportion of sentinel models attacked by birds (34.9% increase in 2018 and 41.1% in 2019), decreased biomass of tree-dwelling arthropods (-51.7%) and reduced probability of apple pest occurrence (from 57 to 40%), compared to orchards without nest boxes.

5. Nesting species showed different predatory roles in apple orchards. Fewer attacks on sentinel pests but lower arthropod biomass was associated with blue tit rather than great tit. Besides, blue tit fed nestlings at a faster rate and included in their diet a higher proportion of apple pests than great tit, which preyed mostly on other herbivorous insects.

6. *Synthesis and applications.* We demonstrated the usefulness of nest boxes for insectivorous birds in enhancing biological control of apple pests at a regional scale, identifying tit species as complementary predators of apple pests and herbivores. From the farmers' perspective, providing nest boxes in orchards may represent an efficient, easy to implement, cheap and attractive measure of ecological intensification, compatible with other actions fostering biodiversity in croplands.

Keywords: apple pests, biological control, blue tit, ecological intensification, ecological restoration, great tit, win-win scenarios

1. Introduction

Sustainable agriculture aims to meet increasing demand for food while reducing the impact of such land use on biodiversity (Tscharntke et al., 2012). This dual goal may be achieved through farming systems that preserve ecosystem services, i.e. ecological processes that impact positively on crops, such as nutrient cycling, pollination, and pest control (Power, 2010). In this context, ecological intensification emerges as a framework to enhance production-supporting ecosystem services (Kleijn et al., 2019). By acting in croplands and their surroundings, farmers can manage specific components of biodiversity to complement, or even replace, artificial inputs like agrochemicals, thereby reducing environmental impacts without decreasing yield (Bommarco et al., 2013). For example, by introducing wild flower strips along field borders, farmers attract pollinators and pest predators, maintaining (e.g. Albrecht et al. 2020) or even increasing (e.g. Pywell et al., 2015; Tschumi et al., 2016) crop yields. Despite the advantages of ecological intensification, its adoption by farmers is frequently hampered by their misconceptions about biodiversity (Penvern et al., 2019), reluctance to interfere with conventional practices or cropping area (Kleijn et al., 2019), or practical constraints, when actions involve land they do not own (e.g. the surrounding landscape; Martin et al., 2019). It is thus crucial to identify efficient, easy to implement measures of ecological intensification across a variety of crop types and environmental settings (Kleijn et al., 2019).

The control of pests by natural enemies is a highly valued service in agriculture (Losey & Vaughan, 2006). Predatory and parasitoid arthropods are traditionally considered highly effective natural enemies, thanks to their frequent trophic specialism, large population sizes, and high diversity which promotes functional complementarity (Dainese et al., 2019; Snyder, 2019). Besides arthropods, insectivorous birds, as generalist consumers with high energetic demand, are also important though frequently overlooked pest predators (García et al., 2020b). In fact, positive effects of bird biodiversity on pest abundance and damage have been demonstrated in different agroecosystems (e.g. Maas et al., 2015; Martínez-Sastre et al., 2020a). However, it remains unclear how ecological intensification may enhance the ecosystem service of insectivorous birds in agricultural landscapes (Lindell et al., 2018). Specifically, research is needed to identify the management measures that provide key ecological resources and conditions (complementary food, nesting sites, habitat complexity) for bird species with high biocontrol potential. Moreover, the effectiveness of bird species for controlling pests may strongly depend on how frequently they prey on other natural enemies, rather than pests, in crops (Grass et al., 2017; García et al., 2020b). Promoting pest control by insectivorous birds thus requires not only ascertaining bird effects under different management options, but also testing for species differences in predatory role.

Artificial nest boxes for insectivorous birds and raptors are a traditional tool for harnessing pest control in agroecosystems (Lindell et al., 2018; Shave et al., 2018). Boxes can increase the density of cavity-nester birds in agricultural habitats, where eliminating old trees to facilitate land use reduces the availability of holes (Jedlicka et al., 2011; Rey-Benayas et al., 2017). Importantly, successful nest box occupancy means the presence of birds with the high food demands associated with nestling feeding, frequently occurring simultaneous to spring outbreaks of pests (Mols et al., 2005; Génard et al., 2017). Indeed, several small-scale studies have found increased insectivory or reduced plant damage in cropland harboring nest boxes with insectivorous birds (e.g. Mols & Visser, 2007; Rey-Benayas et al. 2017). Despite these findings, and the fact that the installation of nest boxes may be seen by farmers as a non-disruptive and low-cost practice (Bardenhagen et al., 2020), we still need to extend our knowledge, at large spatial scales and taking into account differences between bird species and prey types, in order to fully understand nest boxes' potential for ecological intensification.

In this work, we assessed the role of provisioning nest boxes for insectivorous birds on the biological control of arthropod pests in apple orchards in Asturias (NW Spain). Asturian apple orchards are low-input agroecosystems, with high diversity and moderate abundances of arthropods, from pests to natural enemies (e.g. Miñarro et al., 2011), which harbor species-rich bird communities that include cavity-nesters (García et al., 2018). Our general goal was to verify the potential of nest boxes as a tool of ecological intensification, aimed at enhancing the ecosystem service of pest control in apple orchards. As such, we assessed whether i) nest boxes were occupied by insectivorous birds; ii) insectivory, and specifically, pest predation, increased in orchards with nest boxes occupied by insectivorous birds; and iii) nesting species differed in their role as predators of apple pests. To this effect we combined a large-scale experimental assessment of insectivory and arthropod abundance in orchards with and without nest boxes, with fine-scale observations of the preys that birds captured to feed nestlings.

2. Materials and Methods

2.1. Study system

The study was conducted in the apple (*Malus x domestica* Borkh.) crop area of Asturias (NW Spain), a region where almost the entire apple yield (up to 50,000 tons per year) is devoted to cider production. Orchards are typically small (0.5-4 ha) and have a low tree density (250-500 trees/ha). The cultivars are tolerant to common apple diseases (scab, canker and powdery mildew). Growers show high cultural tolerance to pests since many of them are non-professional farmers who are reluctant to pay for spraying (Martínez-Sastre et al., 2020b). Moreover, aesthetic damage is not important for cider apples. Thus, pesticides are used at low frequencies and intensities.

Asturian apple orchards are embedded in a highly variegated landscape and frequently surrounded by natural woody vegetation (García et al., 2018). The low degree of agricultural intensification in many orchards and the surrounding landscape allows for a wide diversity of crop pests and natural enemies. Among arthropod pests (Miñarro et al., 2011), the most prevalent are codling moth (*Cydia pomonella*), aphids (*Dysaphis plantaginea*, *Aphis pomi/spiraecola, Eriosoma lanigerum*) and apple blossom weevil (*Anthonomus pomorum*). Green weevil (*Polydrusus formosus*) is a generalist folivore that frequently attacks apple (Alford, 2007). Natural enemies include birds, spiders, earwigs, hoverfly larvae, predatory beetles and parasitoids (Miñarro et al., 2011). Regarding birds, apple orchards may harbor rich assemblages (up to 32 species) of tree-dwelling insectivores, with robin (*Erithacus rubecula*), tits (*Parus major, Cyanistes* *caeruleus*), thrushes (*Turdus* spp.), blackcap (*Sylvia atricapilla*) and wren (*Troglodytes troglodytes*) being the commonest species (García et al., 2018).

2.2. Experimental design

The study on nest box bird occupancy was conducted between 2018 and 2020. We selected 24 apple orchards distributed over a regional extent of 600 km^2 in central Asturias (Fig. S1A-B). Mean orchard area was 3.2 ha and mean distance between orchards was 8.0 km (minimum 1.3 km). We divided orchards into two experimental groups, a *nest box* group, in which nest boxes were installed, and a *control* group, without nest boxes (Fig. S1C). Due to the high variability in surrounding landscapes, and the effects of this variability on bird and arthropod biodiversity within orchards (García et al., 2018), we first paired orchards with similar proportions of seminatural woody habitat within a radius of 1000 m around the orchard center, and then one orchard of each pair was assigned to each experimental group (i.e. 12 orchards per group; Fig. S2A). This paired allocation resulted in similar geographical distributions for nest box and control orchards (Fig. S1C). More importantly, nest box and control orchards showed similar values of richness (Fig. S2B) and abundance (Fig. S2C) of insectivorous birds within orchards, as well as of abundance of arthropods on apple trees during spring and summer (Fig. S2D), before the start of this study.

Ten boxes were installed in each nest box orchard in December 2017. Seven nest boxes were vandalized during the study but each was replaced at the beginning of the next sampling year (2018-2020; on average, 9.8 nest boxes per orchard per year; min-max 7-11). Nest boxes were tied to the trunk and/or branches of apple trees at a height of 1.8 m, in a line following but at 15 m from orchard edge and separated 20 m from each other. The nest boxes used (Garden Birds Distribuciones, Tarragona, Spain) were made of wood, measured 21.5 x 14.5 x 15.0 cm, and had a 2.6/3.2 cm radius entrance hole (Fig S3A). This type of box, though recommended for tits (Paridae), is occasionally occupied in the region by other species like common redstart (*Phoenicurus phoenicurus*), Eurasian wryneck (*Jynx torquilla*) and Eurasian tree sparrow (*Passer montanus*).

All nest boxes were checked for occupancy by breeding birds in early-May, and cleaned (removal of nest material) and repaired in the autumn-winter period, from 2018 to 2020. Each nest box occupied by breeding birds was considered a *sampling station*, which, in turn, was associated with three *sampling points* —three single trees at 5, 15 and 50 m from the box in a line perpendicular to the edge towards the center of the orchard (Fig. 1). Average (min-max) number of sampling stations in nest box orchards was 2.00 (1-3) in 2018 and 2.58 (1-8) in 2019 (Fig. S1D). Complementing each nest box orchard, an equivalent sampling scheme (in terms of number of sampling stations and points) was replicated in its paired control orchard. For example, a nest box orchard with two occupied boxes led to the establishment of two sampling stations in its paired control orchard (Fig. S1D). As control orchards had no nest boxes to be used as spatial reference, we arbitrarily selected trees at 15 m from the edge to be sampling stations, from which sampling points at 5, 15 and 50 m were established (Fig. 1).

2.4. Bird insectivory and arthropod abundance

We estimated the effects of insectivorous birds in apple orchards through two complementary methods: 1) estimates of bird insectivory based on bird attack on a sentinel pest, mimicked by plasticine caterpillar models (insectivory experiment, hereafter); and 2) measurements of the abundance (biomass and number) of arthropods, and particularly of apple pests, in beating samples from apple trees (arthropod abundance experiment, hereafter). Both samplings were set up simultaneously in all orchards during the period when birds were feeding nestlings (May). The insectivory experiment was conducted two times, in mid-May 2018 and mid-May 2019, whereas the arthropod abundance experiment was conducted only once, in mid-May 2019.

As the sentinel pest mimic we used a green caterpillar model which did not conform to any particular species but resembled the larvae of several pests that attack apple leaves in spring (e.g., *Operophtera brumata*, *Cosmia trapezina*, *Cacoecimorpha pronubana*; Alford, 2007). The caterpillar models were 20-mm long and 3-mm in diameter size, and made from green plasticine (Fig. S3B). They were attached to branches with thin green wire pierced through their longitudinal axis, in a posture imitating natural movement. At each sampling point, we deployed 5 caterpillar models, separated at least 50 cm from each other and on different branches but all at similar heights (1.75 m). They were examined 7 days after set up, and whether they showed signs of bird attack (beak marks on their surface) or had been partially removed (Maas et al., 2015) was recorded (Fig. S3C and S3D). The ground under the supporting branches was also inspected for models which might have fallen 'naturally'. The negligible number of fallen models and the type of damage (no signs of rodent teeth marks were detected) made model removal almost completely attributable to birds (see also Garfinkel & Johnson, 2015; Martínez-Sastre et al., 2020a). For each sampling point, we estimated the number of attacked caterpillar models as those showing signs of attack or having been removed.

To estimate the abundance of tree-dwelling arthropods which could be considered as potential prey for insectivorous birds, we performed a beating sampling for each sampling point tree which entailed selecting two large branches of similar length (>1.5 m long), both at a height of 1.5-m but located on opposite sides of the tree. Three taps per branch were given with a stick, and all fallen arthropods were collected in a plastic tray (80 x 50 x 8 cm) held below the branch. The total fresh biomass of arthropods per sampling point (two branches pooled) was estimated in the laboratory using a precision balance with 0.1 mg accuracy. Arthropods were then counted, identified and classified as well-known apple pests, natural enemies of pests, other herbivores, or indifferent for the crop (such as detritivores). We calculated overall arthropod biomass as well as the total number of individuals in terms of all arthropods, apple pests and natural enemies.

2.5. Feeding activity of nesting birds

We monitored, between 2018 and 2020, the activity of adult birds of different species using nest boxes (great tit *Parus major*, Eurasian blue tit *Cyanistes caeruleus* and common redstart; see Results) to identify the arthropod preys captured for feeding nestlings. For this, we selected 26 occupied nest boxes from 9 orchards, i.e., seven orchards of the main experimental design plus two additional orchards of similar environmental and agronomic characteristics located in the grounds of SERIDA (43° 28' 28.40'' N - 5° 26' 35.00'' W). We made observations of adults on their approach to each of these nest boxes and photographed them. The observer took the pictures holding directly the camera, and being placed at a distance (5-25 m) at which adult birds entered nest boxes without showing reluctance behavior. Photograph sessions on the same nest box lasted 1-1.5 hour, and 1-5 sessions were done per nest box, on different days. We used Nikon Coolpix P900 (Nikon©) and Panasonic Lumix FZ1000 (Panasonic©) cameras. Images were analyzed in the laboratory for prey identification (see Fig. S4 for examples) and classification, according to the functional groups explained above (including pollinators as an additional group). Additionally, in 1-hour observation sessions, we estimated for each breeding pair (i.e. occupied nest box) the number of feeding visits by adults per hour. In this case, to ensure no disturbance to adult behavior, the observer stayed further from the nest box than for photograph sessions.

2.6. Statistical analysis

We evaluated the effect of nest boxes on bird insectivory by means of a Generalized Linear Mixed Model (GLMM; Bolker et al., 2009) using, as a response variable, the proportion of attacked caterpillar models per sampling point (insectivory experiment), considering a binomial error distribution and a logit-link function. As fixed-effect main predictors, we considered orchard group treatment (nest box, control), distance to sampling station tree, and year. Treatment*distance and treatment*year interactions were initially incorporated into the model, but sequentially removed after proving non-significant. The model also incorporated sampling station identity, as well as orchard identity (nested within orchard pair), as random-effect factors.

A similar GLMM procedure was applied to evaluate the effect of nest boxes on the abundance of arthropods in apple trees. Here, we first used a model with the biomass of all arthropods as response variable, considering a gamma error distribution (log function, biomass+1). Second, we used models that took as response variable the number of individuals of different types of arthropods (apple pests, natural enemies, all arthropods). Due to the count-data -and eventually zero-inflated- nature of these variables, and the potential effects on model inference, we preferred not to assume an *a priori* error distribution family for models. Thus, for each of these count-data abundance variables, models with different distribution families were considered: gamma, Poisson, negative binomial and, in those cases with high frequencies of zero values, binomial (i.e. abundance was interpreted from occurrence data), zero-inflated Poisson and zero-inflated negative binomial. The best model for a given count-data abundance variable was taken to be that with the lowest AIC value and the highest AIC weight (Tables S1-S3). All models incorporated orchard group treatment and distance as fixed-effect main factors (interaction term treatment*distance proved non-significant), and sampling station and orchard (nested within orchard pair) identities as random-effect factors.

In order to compare the effect of bird species on insectivory and arthropod abundance, we selected data across orchards from sampling stations occupied by blue tit and great tit (common redstart was excluded from this analysis due to low box occupancy). A GLMM was then used to test the effect of bird species, distance, and year, as fixed-effect main predictors (interaction terms between predictors proved non-significant) on the proportion of attacked caterpillar models per tree (binomial distribution, logit link). A similar procedure was used to check the effects of bird species and distance on arthropod biomass (gamma distribution, log link) and number of individuals (various family distributions, model selection procedure as described above; Tables S4-S6). All models incorporated sampling station and orchard identities as random-effect factors.

Based on observations from adult birds feeding nestlings in nest boxes, we used GLMMs to compare the probability of occurrence of apple pests, and that of apple pests/other herbivores (binomial distribution, logit link), between bird species and years (fixed effects). We similarly checked the effects of bird species and year on the number of feeding visits per hour (gamma distribution, log link). All models incorporated next box identity (nested within orchard) as a random-effect factor.

GLMMs analyses were performed with lme4 (Bates et al. 2015) and glmmTMB (for zero-inflated distributions; Brooks et al. 2017) R packages. Means are shown ± Standard Error (SE).

3. Results

3.1. Use of nest boxes by insectivorous birds

Birds occupied 25.0%, 29.8% and 33.3% of nest boxes in 2018, 2019, and 2020, respectively (range across orchards and years 10.0-80.0%). Great tit was the dominant species each year (2018: 58.6% of occupied boxes, 91.6% of orchards; 2019: 55.6%, 83.3%; 2020: 65.0%, 91.6%), followed by blue tit (2018:

41.4%, 75.0%; 2019: 38.9%, 75.0%; 2020: 25.0%, 66.6%). In both 2019 and 2020, we also recorded one case of breeding by common redstart in one experimental orchard in both years.

3.2. Effect of nest boxes on bird insectivory and arthropod abundance

In the insectivory experiment, the proportion of caterpillar models attacked by birds was significantly higher in nest box orchards than in control ones, with a percentage of increase of 34.9% in 2018 (mean: 0.417 vs 0.309) and of 42.1% in 2019 (mean: 0.540 vs. 0.380) (Fig. 2A; Table 1). Overall attack rate on caterpillar models was higher in 2019 than in 2018 (mean: 0.456 vs 0.361; Fig. 2A; Table 1). We detected no effect of distance on the proportion of caterpillar models attacked (Table 1), indicating that insectivory was maintained up to at least 50 m from the sampling station tree and nest box.

We collected 1627 arthropod specimens in the beating sampling. Among them, there were apple pests (16.7% of individuals), natural enemies (29.3%), other herbivores (11.9%), and arthropods indifferent for the crop (42.0%). Apple pests were aphids (64.4%) and weevils (35.6%). Natural enemies were mostly spiders (64.5%), earwigs (9.8%), parasitoids (8.7%), and predatory bugs (7.6%). In the arthropod abundance experiment, the total biomass of arthropods in the trees of nest box orchards was reduced by 51.7%, relative to control orchards (mean: 40.30 vs. 19.46 mg; Fig. 2B; Table 1). Yet again, distance to the sampling station tree did not affect the biomass of arthropods (Table 1). Concerning the occurrence and the number of individuals of arthropods, a binomial based GLMM evidenced that the probability of occurrence of apple pests on trees significantly decreased from 0.57 in control orchards to 0.40 in nest box orchards (Fig. 3; Table 1; Table S1), and was independent of distance from the sampling station tree (Table 1). Unlike for apple pests, presence of nest boxes in orchards had no impact on the number of individuals of natural enemies or all arthropods together (Fig. 3; Table 1; Tables S2-S3).

3.3. Differences between bird species regarding insectivory and arthropod abundance

The proportion of caterpillar models attacked by birds was significantly higher around nest boxes occupied by great tit (mean: 0.52 ± 0.03) than those occupied by blue tit (mean: 0.43 ± 0.04; Fig. 4A), with no differences due to year or distance (Table 2). Also, arthropod biomass was 58.2% higher around great tit net boxes than around blue tit ones (mean: 22.17 vs. 14.01 mg; Fig. 4B; Table 2). Also, again, no effects of distance, or species x distance interaction on arthropod biomass were observed. Similarly, bird species did not affect either the occurrence of apple pests or the number of individuals of natural enemies or all arthropods around nest boxes (Fig. S5; Table 2; Tables S4-S6).

3.4. Feeding activity of nesting birds

We monitored adult birds carrying arthropods to feed nestlings in 14 nest boxes occupied by blue tit, 15 by great tit and 3 by common redstart. We registered 480 feeding visits and 587 preys, 77.5% of which were identified (Fig. 5).

Blue tit nestling diet included a significantly higher proportion of apple pests (28.4%) than that of the other bird species (Fig. 5; Table 3; see also Fig. S4). In fact, only one apple pest (a blossom weevil larva) was observed among the great tit preys, and none was detected for common redstart (Fig. 5). All three bird species fed nestlings with other herbivores (Figs. S4, S6), this being the most frequent prey type in great tit diet (where it mostly consisted of Lepidoptera larvae: 88%). Thus, considering apple pests and other herbivores together, we found similar frequencies of these arthropods in blue tit and great tit preys, but a significantly lower frequency in common redstart preys (Fig. 5; Table 3). All bird species preyed on natural enemies of apple pests, mainly spiders and earwigs (Figs. S4, S6). Pollinators were preyed by great tit and blue tit in a very low proportion (<3.0%; Fig. 5).

Blue tit showed a significantly higher number of feeding visits per hour per nest box (mean: 42.4 ± 5.3) than either great tit (15.5 ± 2.5) or common redstart (17.5 ± 3.3; Table 3; Fig. S7).

4. Discussion

In the present study, we combined large-scale experiments and fine-scale observations to evidence that the use of nest boxes within apple orchards leads to frequent occupancy by breeding insectivorous birds, increased insectivory rates and decreased arthropod abundances. Importantly, the effects on bird activity also translated into decreased occurrence of apple pests in orchards with nest boxes. Moreover, we show that distinct bird species breeding in nest boxes differed in their insectivore role, especially as regards apple pests. We thus demonstrate that the installation of nest boxes reinforces the ecosystem service of pest control, and may represent an effective ecological intensification measure in woody fruit orchards.

Our research reveals widespread bird occupancy of nest boxes, across a large spatio-temporal extent which encompasses high variability of environmental conditions within and around apple orchards. The physiognomy of Asturian apple orchards, with large trees to which nest boxes can be attached, and well-developed hedgerows surrounding them, fosters the entry of forest-dwelling birds into orchards (García et al., 2018). Notably, nest boxes were exclusively occupied by insectivore species (i.e. no granivore species occurred, e.g. Rey-Benayas et al., 2017). Nest boxes thus lead to increased occurrence of food-demanding insectivores in the season when apple pest infestations typically increase (Miñarro et al., 2011).

Taken together, the different experiments used here suggest that orchards with occupied nest boxes have increased predation pressure on apple pests. On the one hand, models mimicking lepidopteran caterpillars indicate increased insectivory rates attributable to birds, in accordance with previous studies (e.g. Jedlicka et al., 2011; Rey-Benayas et al., 2017). On the other, the beating sampling evidenced that the use of nest boxes decreased arthropod biomass on apple trees. This latter result might seem in conflict with the similar number of individuals of arthropods found in nest box and control orchards, but may well suggest that birds exert a stronger pressure on large preys than on small ones (Jedlicka et al., 2014). Nevertheless, occupied nest boxes significantly reduced the probability of occurrence of pests on apple trees (see also Mols & Visser, 2007). Moreover, our design also evidenced that nest box effects were not restricted to the immediate vicinity but extended further in orchards. Although distance-dependent pest control has been suggested by previous nest box studies focusing on similar spatial extents (e.g. Jedlicka et al., 2011; Rey-Benayas et al., 2017), our results indicate that nesting birds have large foraging ranges (e.g. 5-24 ha in great tit, Caprio & Rolando, 2017), probably facilitated by the wide cover of apple trees (Martínez-Sastre et al., 2020a).

Strong differences between nesting species in insectivore role emerged from our results, thereby extending the findings of previous studies (e.g. Mols & Visser, 2007; Rey-Benayas et al. 2017). Namely, we found fewer attacks on sentinel caterpillars, but lower arthropod biomass, associated with blue tit compared to great tit nest boxes (Fig. 4). The monitoring of adult birds revealed that blue tit fed their nestlings at a very fast rate, and incorporated a high proportion of apple pests, whereas great tit mostly fed nestlings with lepidopteran larvae. Both findings seem congruent in the sense that the higher visitation rate of blue tit could promote greater reductions of arthropod abundance around their nest boxes, compared to other species, while great tit preference for lepidopteran larvae would explain increased attacks on sentinel caterpillar models around theirs (see also Mols et al., 2005). Nest boxes in apple orchards could therefore simultaneously promote a highly effective, but less frequent (in terms of occupancy rate), pest predator – blue tit–, together with a very frequent herbivore predator –great tit. Taking into account too that many of the other herbivores were probably captured on apple trees, we could consider the two tit species to have additive and complementary roles in terms of farming benefits.

Nesting birds also attacked natural enemy arthropods in apple orchards. The proportion of this functional group among preys taken to nest boxes was low, except in common redstart, although its occupancy rate was low. Consequently, nest box use did not actually affect the number of natural enemy arthropods within orchards (Fig. 3). As such, despite some intraguild predation, no evidence of pest liberation from natural enemies (e.g. Grass et al. 2017) was found after putting nest boxes in apple orchards. In the same vein, pollinators were rarely preyed by nesting birds (Fig. 5), even when this functional group is abundant in orchards during nesting season (Miñarro & García 2018), suggesting no negative effect of bird nest boxes on apple pollination is to be expected.

Various studies have questioned the effectiveness of bird nest boxes as a pest control measure, given that they may eventually be occupied by be non-insectivores (Rey Benayas et al., 2017), by insectivores that prey minimally on pests (Jedlicka et al., 2017), or even by birds that favor pests through mesopredator consumption (Grass et al., 2017). In Asturian apple orchards, nest boxes hosted active pest predators belonging to some of the six commoner bird species in this agroecosystem (García et al., 2018).

We recommend, therefore, that farmers install nest boxes in densities similar to that used in our experiments (10 boxes ha^{-1}), as a feasible and effective practice to enhance the ecosystem service of pest control in apple orchards.

Discerning the efficiency of nest boxes as a tool of ecological intensification would require complementary evidence on how the effects of bird insectivory translate into differences in apple yield, data not covered by our study. We have demonstrated elsewhere that avian biological control in apple orchards reduces plant damage by pests (García et al., 2018), and that decreased pest damage leads to increased apple yield (Samnegård et al., 2019). We can therefore assume that farmers are receiving some direct benefit from nest box installation, as well as indirect benefits through decreased pesticide expenses and the consequent amelioration of associated environmental damage (Bommarco et al., 2013). Moreover, farmers may benefit from specific public subsidies for the installation of nest boxes in their orchards. This, in fact, happens in the Asturias region, where biodiversity-friendly orchards can apply for grants of 700 €/ha from the Regional Government to (BOPA, 2020). Thus, several facts should facilitate the quick adoption of nest boxes by farmers. First, farmers are expected to show willingness towards this practice, because nest boxes are cheap and involve no reduction in crop area or conflict with farming practices like pruning, sowing or harvesting. Second, no effect of nest boxes is expected on natural enemy or pollinator arthropods. Thus, this bird-oriented action seems compatible with others fostering pollination and biocontrol by arthropods (e.g. perennial flower strips, Albrecht et al., 2020). And third, grants should be widely available to help farmers implement actions promoting ecosystem services, through policies such as the Common Agricultural Policy (CAP) and the European Union Biodiversity Strategy for 2030. .

Conclusions

The present study demonstrates the usefulness of nest boxes for insectivorous birds in enhancing pest control in apple orchards at a regional scale. Such a positive effect depends on the capacity of nest boxes in crop land to increase the presence of common bird species that are highly effective predators of herbivores and pests. Given that apple, the second most important fruit crop worldwide (FAO, 2020), widely co-occurs with tits (Paridae), abundant in many agricultural landscapes across Europe and Asia (BirdLife International, 2020), we expect our ecological findings to be highly generalizable. Similarly, we also anticipate our findings to be widely applicable, due to apple producers' common perceptions about pest control techniques across Europe (Pervern et al., 2019; Martínez-Sastre et al., 2020b).

Author contributions

DG, MM and RMS designed the study. RMS and MM collected the data. DG analyzed the data. DG and MM wrote the manuscript. RMS revised the manuscript.

Acknowledgements

We thank Alejandro Núñez, Antonio López, Luis Rodríguez and Cristina de Castro for technical support, Ronnie Lendrum for linguistic advice, and all orchard owners for their permission to work in their properties. Funding was provided by grants APCIN2016-000064-00-00 (C-IPM APITREE; MinECo/FEDER) to MM, ClaveSER (Fundación BBVA) and GRUPIN IDI/2018/000151 (Regional Government of Asturias) to DG, and CPD2015-0059 (FPI-INIA) to RMS. Funding sources had no involvement in study design, collection, analysis or interpretation of data, the writing of the report or decision to submit the article for publication.

Data Availability Statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.ht76hdrdn (García et al., 2020)

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Table 1. Generalized Linear Mixed Model evaluating the effect of experimental treatment (control vs nest box), year and distance on caterpillar model attack rates, and on arthropod biomass, the occurrence of apple pests and the number of individuals of natural enemies and all arthropods. In brackets, details of family of error distribution and link function used. Variance for random factors, sampling station and orchard (nested within orchards pair) is also shown.

Sentinel model experiment				
	Predictors	Estimate ± SE/SD	z	P
Proportion attacked caterpillar models (Binomial, logit)	Treatment (nest box)	0.66 ± 0.31	2.10	0.035
	Year (2019)	0.49 ± 0.16	3.12	0.002
	Distance	-0.00 ± 0.00	-1.61	0.108
	Sampling station	0.55 ± 0.74		
	Orchard [Pair]	0.36 ± 0.60		
Arthropod abundance experiment				
	Predictors	Estimate ± SE/SD	t / z	P
Arthropod biomass (Gamma, log)	Treatment (nest box)	-0.44 ± 0.00	-183.25	<0.001
	Distance	0.00 ± 0.00	0.35	0.724
	Sampling station	0.10 ± 0.32		
	Orchard [Pair]	0.16 ± 0.41		
Apple pests (Binomial, logit)	Treatment (nest box)	-0.82 ± 0.35	-2.37	0.018
	Distance	0.01 ± 0.01	1.09	0.275
	Sampling station	0.00 ± 0.00		
	Orchard [Pair]	0.08 ± 0.28		
Natural enemies (Negative binomial, log)	Treatment (nest box)	0.15 ± 0.17	0.84	0.400
	Distance	0.00 ± 0.00	0.43	0.667
	Sampling station	0.01 ± 0.11		
	Orchard [Pair]	0.11 ± 0.33		
All arthropods (Gamma, log)	Treatment (nest box)	-0.12 ± 0.15	-0.82	0.414
	Distance	-0.00 ± 0.01	-0.68	0.494
	Sampling station	0.06 ± 0.25		
	Orchard [Pair]	0.02 ± 0.13		

Table 2. Generalized Linear Mixed Models evaluating the effect of bird species, distance and year on caterpillar model attack rates (sentinel model experiment), and on arthropod biomass, the occurrence of apple pests and the number of individuals of natural enemies and all arthropods (arthropod abundance experiment). Variance for random factors, sampling station and orchard is also shown.

Sentinel model experiment				
	Predictors	Estimate ± SE/SD	z	P
Proportion attacked caterpillar models (Binomial, logit)	Species (great tit)	0.61 ± 0.29	2.08	0.038
	Year (2019)	0.45 ± 0.27	1.65	0.098
	Distance	-0.01 ± 0.00	-1.71	0.088
	Sampling station	0.76 ± 0.87		
	Orchard	0.95 ± 0.98		

Arthropod abundance experiment				
	Predictors	Estimate ± SE/SD	t / z	P
Arthropod biomass (Gamma, log)	Species (great tit)	0.47 ± 0.22	2.12	0.033
	Distance	0.00 ± 0.00	0.76	0.445
	Sampling station	0.04 ± 0.20		
	Orchard	0.17 ± 0.41		
Apple pests (Binomial, logit)	Species (great tit)	-0.46 ± 0.52	-0.93	0.355
	Distance	0.00 ± 0.01	0.40	0.687
	Sampling station	0.00 ± 0.00		
	Orchard	0.53 ± 0.73		
Natural enemies (Poisson, log)	Species (great tit)	0.06 ± 0.20	0.30	0.765
	Distance	0.00 ± 0.00	0.63	0.530
	Sampling station	0.07 ± 0.26		
	Orchard	0.24 ± 0.49		
All arthropods (Gamma, log)	Species (great tit)	0.07 ± 0.18	0.37	0.708
	Distance	-0.00 ± 0.00	-0.24	0.806
	Sampling station	0.07 ± 0.26		
	Orchard	0.03 ± 0.17		

Table 3. Generalized Linear Mixed Models evaluating the effects of bird species (great tit, blue tit and common redstart) and year on the composition of preys taken by adults to feed nestlings, and on the number of feeds per hour. Variance for nest box identity (nested within orchard, random factor) is also shown.

Apple pests (Binomial, logit, N = 383)			
	Estimate ± SE/SD	z	P
Species (great tit)	-5.12 ± 1.12	-4.56	0.0001
Year (2019)	-1.86 ± 1.46	-1.27	0.203
Year (2020)	-3.69 ± 1.22	-3.02	0.003
Nest box [Orchard]	0.30 ± 0.54		
Herbivores and apple pests (Binomial, logit, N = 414)			
	Estimate ± SE/SD	z	P
Species (great tit)	0.06 ± 0.32	0.19	0.849
Species (common redstart)	-2.31 ± 0.57	-4.07	0.0001
Year (2019)	-0.18 ± 0.68	-0.26	0.788
Year (2020)	-0.98 ± 0.61	-1.61	0.107
Nest box [Orchard]	0.02 ± 0.01		
Feeds per hour (Gamma, log, N = 44)			
	Estimate ± SE/SD	t	P
Species (great tit)	-1.59± 0.30	-5.24	0.0001
Species (common redstart)	-0.94 ± 0.50	-1.80	0.050
Year (2020)	-0.67 ± 0.24	-2.81	0.005

Nest box [Orchard]	0.21 ± 0.45

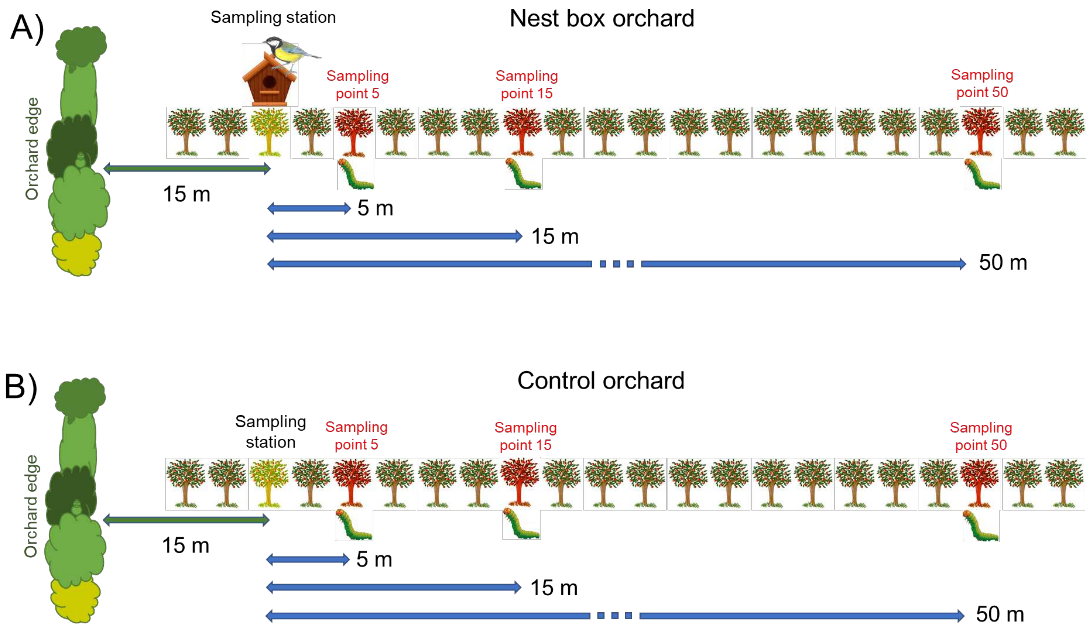

Figure 1. Schematic representation of the sampling design. In nest box orchard (A), ten boxes were positioned in different apple trees at 15 m from the orchard edge and separated 20 m from each other. Each nest box occupied by birds for breeding was considered a *sampling station*, which, in turn, had three *sampling points* –single apple trees at 5, 15 and 50 m from the occupied nest box, in a line perpendicular to the edge and extending into the interior of the orchard. Every sampling station in the nest box orchards had a replicate in the paired control orchards (B), which was established in a tree at 15 m from the edge and had associated three sampling points on trees at 5, 15 and 50 m.

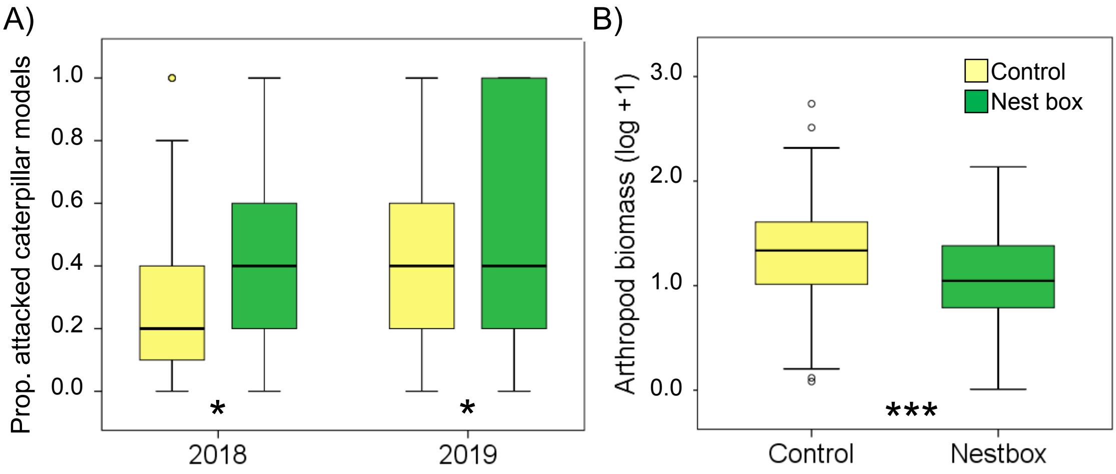

Figure 2. Boxplots representing the proportion of attacked caterpillar models (A) and arthropod biomass (mg) (log + 1 transformed) (B) in control (yellow) and nest box (green) orchards. Asterisks indicate significant differences (*: P ≤ 0.05; ***: P ≤ 0.001) between treatments (see Table 1).

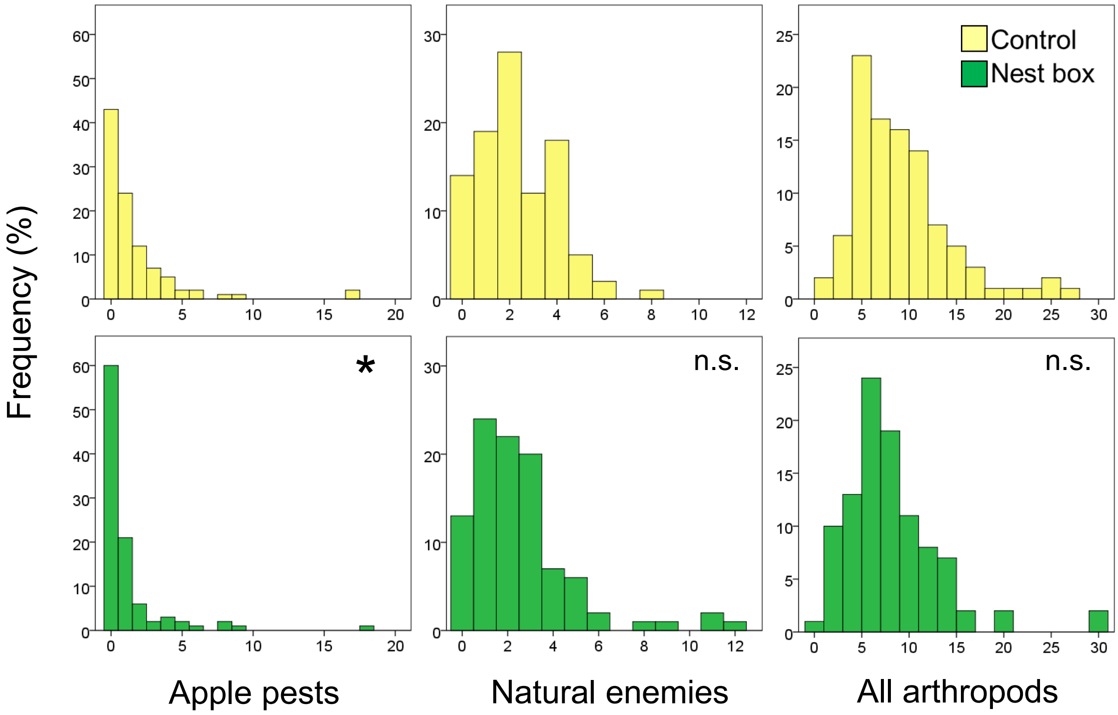

Figure 3. Distribution of the number of arthropod individuals per tree in control (yellow) and nest box (green) orchards. Frequency percentages are shown for apple pests, natural enemies and all sampled arthropods. Marks in lower row indicate statistical differences (*: $P \leq 0.05$; n. s.: $P > 0.05$) between treatments (see Table 1).

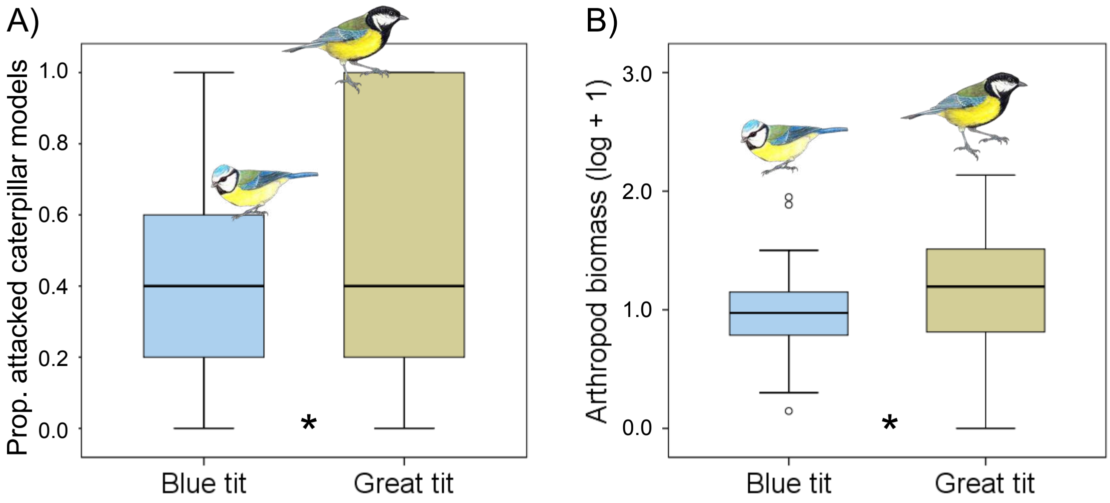

Figure 4. Boxplots representing the differences between bird species in: (A) proportion of attacked caterpillar models and (B) arthropod biomass (mg) (log + 1 transformed) around blue tit and great tit nest boxes. Asterisks indicate significant differences (*: P ≤ 0.05) between species (see Table 2).

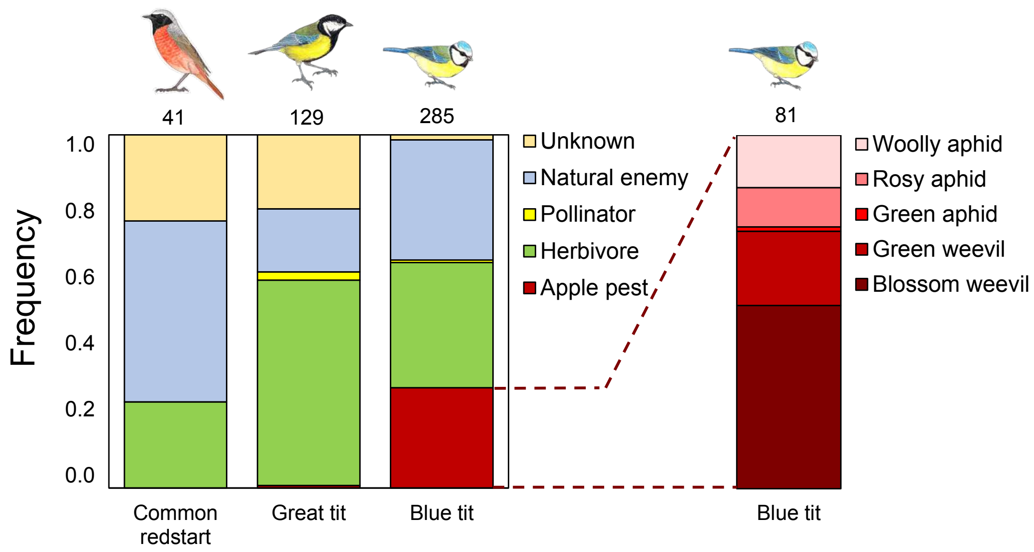

Figure 5. Frequency of preys carried by bird species to nest boxes, according to prey functional group and with details of apple pests. The number of identified preys is indicated above each column. Artwork by Daniel García.