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Vertebrate frugivory in blueberry crops: Patterns across birds and mammals and consequences for yield

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ABSTRACT

Damage and consumption of crops by vertebrates represent a significant source of conflict between humans and wildlife. This is particularly relevant in the context of small-fruit crops, such as blueberries, which are highly conspicuous, small-sized, and situated close to the ground, allowing a wide range of vertebrate species to swallow them whole and in large quantities. In the present study, we assessed the patterns of blueberry consumption by birds and mammals, and the effect of consumption on crop yield, in blueberry orchards in northern Spain. To this end, we characterised the fruit-eating vertebrate community through direct observation and camera traps in blueberry orchards, and conducted exclusion experiments in blueberry cultivars that ripen at different dates. The study was conducted in eight orchards over two consecutive years. We recorded 14 bird species and four mammal species consuming blueberries, with common blackbird (*Turdus merula* L.) and wild boar (*Sus scrofa* L.) accounting for more than 80 % of consumption events. Whereas frugivory by blackbirds was observed across orchards and cultivars, blueberry foraging by wild boar was highly localised. The exclusion experiments evidenced a negative impact of vertebrate frugivory on blueberry production. However, this impact was not homogeneous across sites, ranging from no impact to 74 % of yield loss. Similarly, vertebrate impact depended on the cultivar, with the early ripening cultivar being more susceptible to yield losses than late ripening cultivars. Further research is needed to ascertain what extrinsic (orchard and landscape structure) and intrinsic (abundance and physiological requirements of vertebrates) factors are responsible for the observed variability in yield loss across sites and cultivars. In terms of management, we recommend to prioritise bird deterrent methods to minimise the negative impact of vertebrates.

1. Introduction

Birds and mammals are responsible for ecosystem services and disservices in agroecosystems (e.g. Civantos et al., 2012; Pejchar et al., 2018; Tschumi et al., 2018). The suppression of insect and vertebrate pests and the pollination of crops are among the most recognized ecosystem services provided by vertebrates to agriculture (e.g. Civantos et al., 2012; Kross et al., 2012; Pejchar et al., 2018). Conversely, the consumption of crops, the spread of pathogens or the antagonistic interaction between insectivorous vertebrates and predatory arthropods — resulting in the release of pests from mesopredators — are disservices that can frequently occur on agricultural land (e.g. Anderson et al., 2013; Grass et al., 2017; Gonthier et al., 2019). In a context of human-wildlife conflict, crop damage represents a significant challenge that can result in substantial economic losses (Gebhardt; Anderson et al., 2013; McKee et al., 2020) and even compromise the food security of local communities (Raphela). Furthermore, after a negative experience with fauna damaging their crops, farmers tend to develop a negative perception of biodiversity that can ultimately jeopardise the success of biological conservation efforts (Redpath et al., 2015; Delibes-Mateos et al., 2020). In the case of fruit crops, the impact of frugivorous vertebrates is of particular relevance due to their important direct effects on yields via fruit consumption (Anderson et al., 2013; Cassano et al., 2021; Monteagudo et al., 2023a). However, the ecosystem disservice by vertebrate frugivores seems to have been globally underestimated due to a lack of research on the topic. This is partly because, unlike insects, weeds or diseases, birds and mammals are viewed as charismatic species and are often seen from the aspects of biodiversity conservation and

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ecosystem services and more rarely as pests (Sausse).

Blueberries are among the crops that often suffer from bird frugivory, resulting in significant yield reduction and economic losses (Anderson et al., 2013; Peisley et al., 2015; Lindell et al., 2018a). Blueberry is a relatively recent and rapidly expanding crop in temperate locations like Spain. This country is already the leading blueberry producer in Europe (70,420 t in 2022) and the fifth largest producer in the world, after the USA, Peru, Canada, and Chile (Faostat). Most Spanish blueberry production comes from southern Mediterranean sites (De Pablo et al., 2016). However, the complementary production of northern, Atlantic Spain is of great strategic importance, as the harvesting occurs during summer, when the southern production has already ceased. Blueberry crops in northern Spain are typically planted with cultivars of two species: the northern highbush blueberry (*Vaccinium corymbosum* L.) and the rabbiteye blueberry (*Vaccinium ashei* Reade), both native to North America (García). The introduction of such exotic crops into regions distant from their origin requires adaptation to the edaphic and climatic conditions of the new farming environment. Similarly, the new crop has to deal with the local fauna, both beneficial animals providing services, such as pollination (Miñarro), and detrimental fauna potentially damaging the crop, such as vertebrate frugivores (e.g. Anderson et al., 2013; Lindell et al., 2018a).

Despite being exotic, blueberry crops have certain characteristics that make them susceptible to heavy attack by a diverse array of autochthonous vertebrate species. First of all, the fruits are conspicuous, soft and small in size, allowing many animals to swallow them whole and in large quantities. Secondly, plants are short in height and fruits are produced close to the ground, thus allowing easy access to vertebrate species with a wide range of foraging strategies, from small, perching birds to large, ground-dwelling mammals (Garcíaíguez et al., 2022). And thirdly, blueberry orchards provide a reliable and sustained food source over time thanks to the coexistence of cultivars with overlapping ripening times (García). Consequently, the range of potential blueberry consumers in northern Spain may be wide, given the diversity and abundance of native frugivorous birds and mammals (Peredo; Rumeu et al., 2020). Accordingly, it becomes crucial to better understand the magnitude and the patterns of fruit consumption by different vertebrates in blueberry plantations of northern Spain. Ascertaining the differential frugivore roles of bird and mammal species is required to develop successful measures of pest deterrence or control. Thus, we specifically addressed the following questions: 1) Do native birds and/or mammals feed on blueberry crops? 2) Does vertebrate frugivory depend on the ripening time of the cultivar? and 3) Does vertebrate frugivory have a widespread detrimental effect on the blueberry yield? To answer these questions, we characterised the fruit-eating vertebrate community through direct observation and camera trapping and conducted an exclusion experiment to estimate the impact of fruit removal by vertebrates on blueberry yield in two consecutive years.

2. Materials and methods

2.1. Study system

The study was conducted in the region of Asturias, in northern Spain (43°20N, 6°00W; Fig. A.1A). Asturias has a temperate oceanic climate, with rainfall usually in excess of 1100 mm and fairly evenly distributed throughout the year. The region encompasses a wide topographic gradient, with altitude ranging from 0 to 2500 m a.s.l. The experimental blueberry orchards were small (mean: 1.7 ha; range: 0.5–3.7 ha), and located on terrain with variable slope, at altitudes ranging from 50 to 800 m a.s.l. All blueberry orchards are planted with two or more cultivars to cover a larger market window. Normally, fruit ripening starts at the end of May and lasts up to September. Most blueberry crops are grown outdoors without covering structures. There is, however, an increasing number of growers who are installing permanent or temporary plastic covers to advance fruit ripening, facilitate harvesting on rainy days and reduce pest attack (García). Regarding landscape composition, blueberry crops are embedded in a fine-grained mosaic of pastures, crops, eucalyptus plantations and patches of natural woody vegetation, from hedgerows separating fields to forests or shrublands surrounding orchards (Miñarro). Asturian blueberry orchards are not yet affected by arthropod pests that have important effects on production, except the recently introduced spotted wing drosophila (*Drosophila suzukii* Matsumura; García et al., 2018). However, in recent years, blueberry growers in Asturias and neighbouring regions have been increasingly reporting yield losses caused by birds (personal communications and García et al., 2018).

2.2. Field procedures

In 2022 and 2023, we conducted field observations to quantify blueberry fruit removal by vertebrates, and an exclusion experiment to assess frugivory effects on crop yield. Each year, we worked in eight blueberry orchards, with five of these being common to both years. All the orchards in the study were uncovered. In each orchard, we selected two blueberry cultivars to account for different fruit ripening dates: a cultivar ripening in June (hereafter early cultivar), which was ‘Duke’ (northern highbush) in all cases, and a cultivar ripening in August–September (hereafter late cultivar), which was most frequently ‘Ochlockonee’ (rabbiteye), but also ‘Centrablue’ (rabbiteye) and ‘Aurora’ (northern highbush) in some orchards where ‘Ochlockonee’ was not present. In 2023, late cultivars were only available for study in five of the eight orchards.

In both years, we made frugivory observations during the ripening period of each target cultivar in order to ascertain the vertebrate species that feed on blueberries and their consumption behaviour. We employed two different, complementary monitoring methods: direct observation and camera trapping (Acevedo-Quintero et al., 2020). Direct observation entailed the visual recording of frugivory for 1 h, between 7:00 and 12:00, in each cultivar and orchard by an observer positioned at the end of the plant rows. We recorded the vertebrate species identity, the time of consumption, the number of fruits consumed and whether the animals picked the fruit from the ground or directly from the plant. For camera trapping, we placed one camera (Alpha Cam Premium) in each orchard during the ripening period of each target cultivar. We considered using a single camera the most cost-effective option, given the limited size of the study orchards (0.5–3.7 ha), the small number of rows of the selected cultivars per orchard (2–5), and the high mobility of the target species. The cameras were positioned at the end of an alley with unobstructed visibility along its entire length, with plants of the target cultivar on both sides. Each camera was attached to a PVC pole at a height of ca 1m (Fig. A.1B), and functioned non-stop, being activated by movement and recording 30-s videos with 20-s intervals between each recording. All cameras were operational for at least one week in each cultivar and orchard, with an average of 280.7 ± 125.5 h of recording. Subsequently, the videos were meticulously reviewed to record the same parameters of vertebrate frugivory as those employed in direct observation.

We assumed both monitoring methods to be mutually reinforcing. Direct observation allows for a more comprehensive description of avian communities and facilitates comparison between sites. However, it is less effective in identifying elusive species, such as mammals, and is time-constrained, which hampers the observation of temporal patterns. In contrast, camera trapping is a non-invasive method that also enables the detection of mammals and that can be employed effortlessly for long periods. However, the effectiveness of this method depends on the position and orientation of the camera to achieve satisfactory records (Acevedo-Quintero et al., 2020; Ortmann and Johnson, 2020). In the case of birds, we were able to quantify the number of blueberry fruits picked and consumed in both direct observation and camera recordings. Each feeding bout corresponded to one fruit picked and later consumed. However, in the case of large mammals, which bite fruit clusters directly from branches, we could not ascertain the exact number of fruits consumed in the same feeding bout. Consequently, we quantified consumption event records as the number of feeding bouts performed by a given species in each individual blueberry plant. For analysis purposes, and for each species, we pooled the data of consumption events from both methods (direct observation and camera recording). Previously, we standardised them according to the respective sampling effort (observation hours). For direct observations, the sampling effort was 1 h in every case. In the case of camera trapping, it was the number of hours in which the camera was active in each cultivar and orchard. The sampling effort per day was also adjusted for birds and mammals independently, based on the hours in which >95 % of the records of each animal group occurred: 14 h per day (7:00 a.m. - 8:00 p.m.) and 10 h per day (9:00 p.m. - 6:00 a.m.) for birds and mammals, respectively. Finally, we calculated a metric of frugivory records per hour of observation.

For the exclusion experiment, in each orchard and cultivar, we selected eight blueberry plants similar in size and apparent fruit load. The selected plants were spaced at least three plants apart. Plants were randomly assigned to one of two treatments: excluded and open. The plants in the excluded group were individually enclosed within a 2 m^3 cage (1 m × 1 m base x 2 m high) made with a frame of PVC tubes and nylon mesh (20 × 20 mm pore) to preclude access by vertebrates to fruits (Fig. A.1C). Plants in the open group were left uncovered and accessible to vertebrates. All plants in the experiment were marked and identified with a visible tag. To assess the impact of frugivory on blueberry yield, we monitored production by measuring the fresh weight of fruit harvested from each experimental plant. The fruits were harvested progressively as they ripened. Some experimental plants were accidently harvested by farm workers prior to recording yield data and, thus, data from both cultivars in one orchard in 2022, and from the early cultivar in one orchard in 2023, were unavailable. Given the yield variability between plants of the same treatment observed in 2022 in certain orchards, in 2023 we estimated the potential yield of a given plant by counting the number of unripe fruits.

2.3. Statistical analyses

We estimated the temporal frequency of blueberry consumption by birds and mammals throughout the day using kernel density. To avoid the over-representation of the specific hours in which the direct observations were conducted, we only employed data from the camera trapping. We quantified the extent of temporal overlap in blueberry consumption between birds and mammals with the functions *overlapEst*, *bootstrap* and *bootCI* in the R package overlap (Meredith et al., 2024). Furthermore, we utilised the function *overlapPlot*, included in the same package, to represent the kernel density functions. The coefficient of overlapping is defined as the area under the lower of the two density functions. This coefficient ranges between 0 and 1, with 0 representing no overlap and 1 representing complete overlap (Meredith et al., 2024). In contexts where there is a high degree of temporal overlap, it is essential to identify the daily moments when birds and mammals co-occur. This information is crucial for the design of management strategies that target both groups.

We evaluated the effect of vertebrate fruit removal by comparing the yield of open and excluded plants in the exclusion experiment for both cultivars. We adjusted a generalized linear mixed model (GLMM), with gamma distribution and log link function. The yield of each experimental plant was employed as the response variable, with treatment, cultivar, their interaction, and year as explanatory variables. We included the orchard identity as a random effect variable. Then, we applied a Tukey post-hoc test to look for differences between the four possible treatment-cultivar combinations. In order to ensure that the observed yield effects were independent of within-treatment, inter-plant variability, a similar model was adjusted only for the 2023 data. This incorporated the number of unripe fruits (scaled) into the fixed effects as a covariate. We fitted the model through the *glmer* function from R package lm4 (Bates et al., 2015). The model adequacy was checked by visual diagnosis (residuals vs fitted values plot, and quantile-quantile plot), and that the model fit was assessed by calculating the conditional and marginal coefficient of determination using the function *r.squaredGLMM* in the package MuMIn (Bartoń).

Finally, we assessed whether higher frugivory levels resulted in higher yield losses. As a measure of yield loss, we used the open treatment yield expressed as a percentage of the excluded treatment. We conducted a Pearson correlation analysis between the number of frugivory records per hour of observation and the percentage of losses for each cultivar and orchard in both years. We aggregate frugivory records based on year, orchard, and cultivar, and adjusted in accordance with the sampling effort applicable to each case. Then, frugivory records were log-transformed to normalise the distribution. All analyses were performed in R version 4.2.1 (R Core Team, 2022).

3. Results

3.1. Blueberry fruit removal by vertebrates

We recorded a total of 3277 observations (71.2 % of birds and 28.8 % of mammals) involving 36 different vertebrate species in the blueberry orchards, 30 of which were birds (Table A.1). Of these, 1454 were identified as consumption events, involving 14 bird species (50.9 % of the consumption events) and four mammal species (49.1 %; Table A.1; Fig. 1A). The early ripening cultivar accounted for 95.1 % of the consumption events (Fig. 1A). Blueberries were picked both from the ground (57.4 % of the consumption records) and directly from the plant (42.6 %) (Fig. 1B). Wild boars (*Sus scrofa* L.; Fig. A.2A) (48.6 %) and common blackbirds (*Turdus merula* L.; Fig. A.2B) (34.7 %) were responsible for the vast majority of the 1454 observed consumption events (Fig. 1A; Table A.1). We recorded fruit consumption by wild boars only in four of the 11 orchards, with 81.7 % of these events occurring in a single orchard for the early cultivar (Table A.1). Wild boars consumed blueberries mostly from the ground (68.0 % of consumption events; Fig. 1B). In the case of blackbirds, consumption events were recorded in almost every orchard for both cultivars (Table A.1), and equally distributed between the ground (49.3 %) and the plants (50.7 %). (Fig. 1B).

We observed great differences between birds and mammals in the daily patterns of fruit consumption in blueberry orchards (coefficient of overlapping, Dhat4 = 0.061, CI = 0.035–0.059; Fig. 2). Birds were recorded eating blueberry crops from just before dawn to dusk, most frequently in the morning and midday (between 10:00 a.m. and 2:00 p.m.; Fig. 2). The pattern of mammals exhibited two marked peaks of activity, one occurring close to dawn and the other close to dusk (at 6:00 a.m. and 10:00 p.m., respectively; Fig. 2).

3.2. Effects of vertebrate frugivory on blueberry yield

We found significant effects of frugivore exclusion, cultivar type and year on the blueberry yield, as suggested by the generalized linear mixed model (Table 1). Yield was higher in the early cultivar (1900.3 ± 117.0 g) than in the late one (1467.5 ± 102.1 g; $p < 0.001$). Furthermore, the yield was also higher in the excluded plants (1872.7 ± 120.7 g) than in the open ones (1589.2 ± 112.6 g; $p < 0.001$), attributable to a negative impact of vertebrate frugivory on blueberry yield in the open plants. The overall percentage of yield loss was 13.1 ± 5.1 %, but with considerable variation among orchards and cultivars (Fig. 3), with losses reaching as high as 74.4 % in one particular case. The post-hoc test confirmed a significant effect of treatment in the early cultivar (2117.6 ± 168.1 g in the excluded plants vs. 1683.0 ± 159.1 g in the open plants; $p < 0.001$) but not in the late cultivar (1491.7 ± 144.7 g vs. 1443.3 ± 146.1 g for excluded and open plants, respectively; $p = 0.531$) (Fig. 4; Table 1). When accounting for the variability in yield among plants by including the number of unripe fruits in the analyses, the results remained consistent. We can therefore discard any effect of inter-plant variability

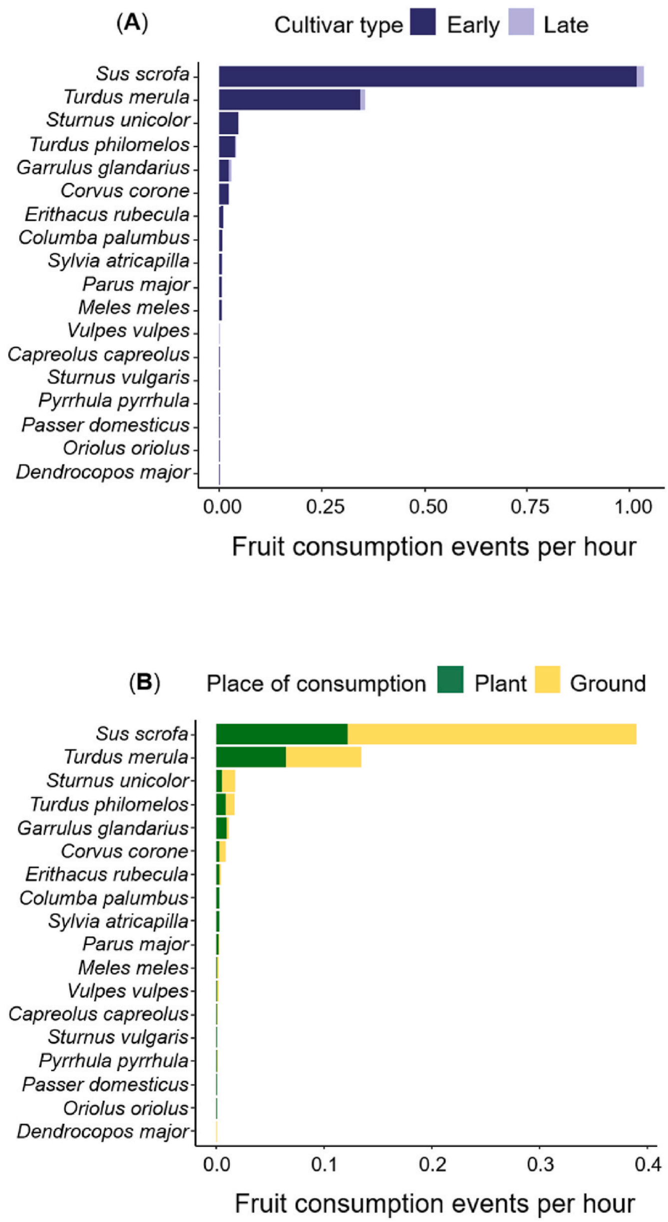

Fig. 1. Fruit consumption events, adjusted by sampling effort, in blueberry orchards for each vertebrate species according to (A) the cultivar type and (B) the place of consumption.

in the yield of the target plants (Table A.2).

No correlation was observed between the percentage of yield loss and the number of records of fruit consumption per hour (Pearson correlation coefficient, r = 0.007; p-value = 0.976; N = 22). Therefore, blueberry yield losses across orchards and cultivars were independent of the magnitude of frugivory (Fig. A.3).

4. Discussion

In the present study, we aimed to evaluate the patterns and the impact of frugivory by vertebrates on blueberry crops in northern Spain. We recorded the consumption of blueberries by 18 different species of birds and mammals, with one mammal, the wild boar, and one bird, the blackbird, accounting for more than 80 % of consumption events. The exclusion experiment confirmed a net negative impact of vertebrate frugivory on blueberry production. This impact was, nevertheless, inconsistent between sites and cultivars, with early ripening cultivars being more susceptible to suffering this ecosystem disservice.

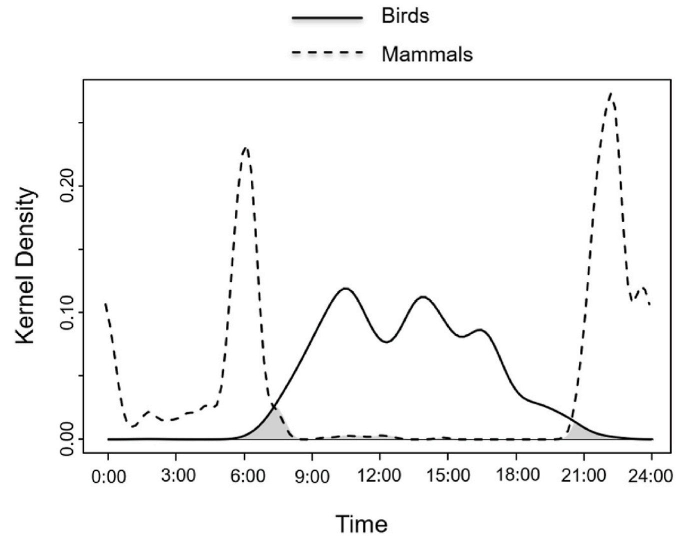

Fig. 2. The daily patterns of fruit consumption events by birds and mammals in blueberry orchards, obtained from the camera trap records. Shaded area represents the overlap between both groups.

Table 1
Results of the generalized linear mixed model (GLMM), with gamma distribution and log link function, evaluating the effect of the exclusion experiment and the cultivar type on blueberry yield per plant in 2022 and 2023.

Fixed effects	Estimate	SE	t	p	R^2m	R^2c
(Intercept)	7.301	0.218	33.461	<0.001	0.207	0.472
Treatment: Excluded	0.259	0.078	3.323	<0.001		
Cultivar: Late	−0.339	0.091	−3.708	<0.001		
Year: 2023	−0.308	0.071	−4.322	<0.001		
Treatment: Excluded | Cultivar: Late	−0.198	0.124	−1.603	0.109		
Random effects	Variance	SD				
Orchard	0.089	0.298				
Residual	0.163	0.404				
Tukey post hoc test	Estimate	SE	z	p		
Early: Open - Excluded	−0.259	0.078	−3.323	<0.001		
Late: Open - Excluded	−0.060	0.096	−0.626	0.531		

4.1. Blueberry fruit removal by vertebrates

Most studies on fruit consumption by vertebrates focus on birds (e.g. Anderson et al., 2013; Lindell et al., 2018a; Hannay et al., 2019), in part because bird frugivory is more noticeable (for both growers and researchers) given the diurnal activity of birds (Anderson et al., 2013). The consequent methodological approach usually employed in frugivory studies (direct observation; Lindell et al., 2018a; Gonthier et al., 2019; Hannay et al., 2019) does not allow the frugivory activity of mammals, which are typically nocturnal, to be captured. The methodology used in this study, complementing direct observation with the use of camera traps, allowed us to confirm that wild mammals may also be important pests of blueberry crops. We recorded in fact four mammal species feeding on blueberries, but one of them, the wild boar, accounted for 98.9 % of the frugivory events by mammals. However, although the wild boar was the animal with the highest rate of fruit consumption, crop damage by this species was highly contingent on space and time. The records of consumption by this species were mostly concentrated in the

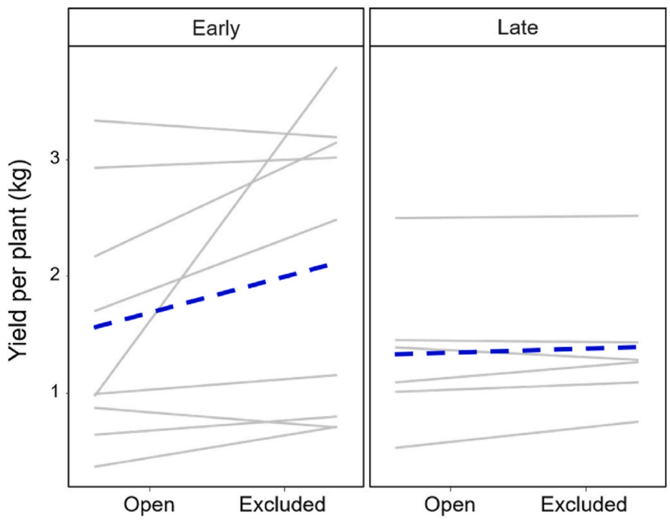

Fig. 3. Yield per blueberry plant by cultivar, for the open and excluded experimental treatments (different grey lines for different orchards and blue dashed line for the average value for all orchards). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

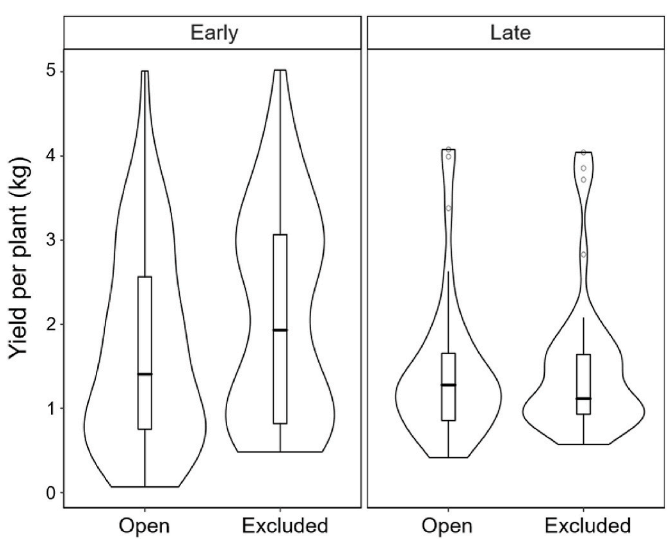

Fig. 4. Violin plots and boxplots representing the distributions of the yield per blueberry plant for the open and excluded experimental treatments in the early and late ripening cultivars.

early cultivar in one specific orchard in 2022. In contrast, frugivory by birds, and, in particular, by the ubiquitous common blackbird, was observed in all sites and on both cultivars. Thus, we can consider blackbirds as the primary vertebrate responsible for blueberry consumption in our region, with other bird species exerting a comparatively minor influence. These findings are consistent with those from other regions, where thrushes (Family Turdidae, which includes common blackbird) are significant pests of small fruits, such as berries, cherries and grapes (Kross; Lindell et al., 2018a; Hannay et al., 2019). The common blackbird is a widely distributed and abundant bird species in the study region (García; Rumeu et al., 2020), able to display a variety of behavioural adaptations, including the capacity to track fluctuations in fruit availability over time and space (MartínezGarcía). In addition, its body size and morphological adaptations, such as the possession of beaks wider than those observed in non-frugivorous species (Herrera, 2004), allow this species to swallow the blueberry whole.

Interestingly, we recorded an overall higher frequency of consumption events on fruit fallen on the ground than on fruit still attached to blueberry plants, which was particularly marked for wild boar. Fallen fruit may have been dropped by the vertebrates themselves when foraging, but may also have fallen to the ground due to the action of wind or rain or the harvesting activities of farm workers. In any case, part of this fallen, unharvestable fruit could already be infested, or even still be a resource for oviposition, by the key blueberry pest *D. suzukii* (Stemberger; Schöneberg et al., 2021). In fact, the removal of fallen fruit from plant surroundings is recommended as a crop husbandry control measure against this pest (Schöneberg) even when manual removal requires a considerable amount of labour. Thus, the spontaneous removal of fallen fruit by vertebrates, thereby reducing the likelihood of an increase in *D. suzukii* infestations in the crop, may be considered as a free phytosanitary protection process that could partially compensate for crop yield loss. Moreover, most birds observed eating blueberries during the present study have a wide diet, including insect crop pests, at other times in their annual life cycle (García). Further research on the different ecosystem services and disservices that these vertebrate species might perform in relation to the crop would help to better understand the service net balance and the role that these species play in this agroecosystem (Pejchar; Garcia et al., 2020).

4.2. Effects of vertebrate frugivory on blueberry yield

The exclusion experiment confirmed that the consumption of blueberries by birds and mammals reduces crop yield. Yield loss seems to be a common issue in crops of small sweet fruits that can be easily handled and swallowed by birds, such as blueberry, cherry or grape (Kross; Anderson et al., 2013; Peisley et al., 2015; Lindell et al., 2018b). We found, however, a considerable variation between orchards with respect to the percentage of losses due to vertebrate frugivory, ranging from orchards that were almost unaffected to others that lost three quarters of the yield of some cultivars. It is worth noting that this heavily damaged plantation had no wild boars, with the damage caused only by birds. The early-ripening Duke cultivar suffered more frugivory than the late ripening ones (mainly Ochlockonee), which showed no difference in production between open and enclosed plants. This seasonal effect could be due to the attraction and palatability of the variety itself (Blendinger) but also to the ripening phenology in relation to vertebrate population dynamics. The higher vulnerability of early-ripening blueberry cultivars to avian predation has been documented previously (Nelms; Tobin et al., 1991).

The observed differences in frugivory pressure across orchards and cultivars were probably contingent upon a multitude of factors, both extrinsic and intrinsic. With regard to extrinsic factors, the landscape and orchard features, as well as alternative resource availability, are of particular importance (Sausse). At the landscape level, a higher landscape complexity is frequently associated with a reduction in frugivory-related disservices in agroecosystems (Gonthier). In our case, and at least for other fruit crops such as apple plantations, it is known that the abundance of wild birds (including all frugivore species shown here) increases in fruit orchards surrounded by a higher cover of semi-natural woody habitats like forests and hedgerows (García). Ascertaining whether landscape effects on bird abundance lead to higher frugivory levels and, more importantly, are generalized to blueberry orchards, would require a set of orchards larger than that studied here and representative of a wide gradient of landscape characteristics. Another extrinsic factor is the availability of alternative food (fruit) resources in the habitat surrounding blueberry orchards. Fruiting in the hedgerows is significantly lower during the ripening of the early cultivar, as the majority of the native fleshy-fruit species present in the area begin to ripen in the middle or end of summer (Fernández; García et al., 2024).

The intrinsic factors acting on frugivory include the frugivore population dynamics and the physiological requirements of the animal species, which vary according to their breeding status (Sausse). In our case, the maturation of the early cultivar (June) overlaps with the end of the breeding season for a significant proportion of bird species present in the study area (e.g. blackbirds, Aparicio, 2016; the song thrush *Turdus philomelos* Purroy and Purroy, 2016; the Eurasian jay *Garrulus glandarius* L., Alonso, 2016). This is relevant, because many of our frugivore observations belonged to numerous blackbird post-fledging juveniles, still following adults into blueberry orchards before individual dispersal (see also Hampe, 2001).

Even though our findings indicate that generalist common birds may cause yield losses in the blueberry orchards that were studied, we found no correlation between the number of observed frugivory events and the percent of yield losses across sites and cultivars. This may be attributed to the inherent limitations of camera trapping, as the efficacy of this method in recording frugivory events depends on camera position and orientation (Acevedo-Quintero et al., 2020; Ortmann and Johnson, 2020). Consequently, observations of frugivory, conducted in accordance with the methodology outlined in this study, are a valuable tool for establishing patterns of frugivory across vertebrate species, but they have limited value for estimating the agronomic impact of frugivory.

4.3. Conclusions and recommendations for management

Blueberry orchards in northern Spain are susceptible to yield losses associated with vertebrate frugivory, particularly on cultivars ripening in late spring-early summer. Yield losses are primarily caused by birds, although wild boars may be also the main cause of crop damage in certain cases. Significant yield losses due to vertebrates were not generalized across cultivars and orchards in the region. This means that although farmers might observe birds frequently feeding on their blueberry crops, this does not necessarily imply significant yield losses in all cases. Thus, frugivory observations are not useful for anticipating or explaining the magnitude of yield loss.

A variety of visual and acoustic devices (propane cannons, decoys that resemble raptors, reflective tapes) are commonly used as deterrent tools against frugivorous birds. However, these methods are often ineffective, primarily due to the capacity of birds to habituate (Cook et al., 2008; Lindell et al., 2018a; Lindell, 2020). The combination and rotation of these techniques could counteract in part the habituation effect (Rivadeneira). Other techniques that result in the occasional death of individuals demonstrate lower levels of habituation (Cook et al., 2008), but, beyond ethical issues, lethal control is prohibited in the European Union for the majority of species involved in blueberry damage (Directive 2009/147/EC, 2009). The most effective tactic is probably preventing access of vertebrates to the crops. Nets or plastic covering all the crop may completely exclude frugivorous birds. The partial plastic covers already implemented in some blueberry orchards in Asturias (with lateral and frontal parts uncovered to facilitate crop ventilation) have the potential to deter many bird species reaching the crop by high-level flight (such as pigeons or starlings) but are probably not so effective against ground- and low vegetation-dwelling bird species, such as blackbirds. The implementation of exclusion methods that cover all the crop may be prohibitively costly (Lindell, 2020). Exclusion of wild boars and other mammals with the use of electric fences seems to be simpler and cheaper than bird exclusion (Reidy et al., 2008).

Habitat management strategies may also reduce bird-related damage (Lindell, 2020). The installation of perches and nest boxes may create landscapes of fear for frugivorous birds by enhancing the presence of raptors in the crops and their surroundings (HYPPeisley; Shave et al., 2018). At the landscape level, an increased proportion of woody habitats surrounding the orchards would provide shelter for ornithophagous raptors which could utilise the crops as foraging habitats (Monteagudo). The use of falconry, or even robotic falcons, could be an alternative to create landscapes of fear in the crop (Steensma; Egan et al., 2020). These and other avian deterrent strategies could be primarily implemented in the morning, when frugivorous activity in birds is most concentrated. Additionally, increasing the availability of alternative resources for birds in the form of wild fleshy-fruited plants ripening during the targeted season could also reduce the frugivory pressure on the crop (Rivadeneira; Montgomery et al., 2020). Even the presence of blueberries on the ground can also serve as diversionary food for vertebrates, diverting them from the blueberries on the bushes. Empirical evidence of the differential effectiveness of most of these control methods, the cost-benefit analysis of their implementation, and the consequences they may have on the provision of agricultural ecosystem services by the target (or other) vertebrate species are still lacking and need further research (Anderson et al., 2013; Lindell et al., 2018b).

CRediT authorship contribution statement

José Javier Jiménez-Albarral: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Daniel García:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Marcos Miñarro:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2025.107213.

Data availability

Data will be made available on request.

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