Bird-mediated damage in English vineyards is modest and spatially structured, with no detectable effect on yield.

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Open research statement

Raw data will be archived in the Dryad digital repository and the link will be made available with the article.

Key words

grape damage, frugivory, organic management, ecosystem disservices, viticulture, sustainability

Abstract

Biodiversity in agricultural landscapes provides both ecosystem services and disservices, and understanding its net effect on production is essential for sustainable management. Birds are often perceived as pests in fruit-growing systems, but their overall impact is context-dependent. Viticulture is expanding in the United Kingdom, where bird-mediated grape damage is considered a challenge. Here, we assessed the effect of birds on production across English vineyards spanning gradients of landscape complexity and management practices. We combined grape damage assessments, experimental exclusion and bird surveys to quantify bird-mediated grape damage and relate it to yield. Overall, bird damage was modest (3.8% per bunch) and strongly spatially structured, peaking at around 20% damage per bunch at the field edge and declining to ~5% at 40 m from the edge. Damage was not related to the abundance of grape-eating bird species, and varied substantially among sites and years. Damage increased with semi-natural habitat cover and ground vegetation, but showed no relationship with wooded edges, suggesting that habitat structure and easy access into the crop, rather than habitat type or abundance, underpin frugivory patterns. Importantly, our models showed no correlation between bird-mediated grape damage and yield, which instead varied markedly between management approaches (51% lower yield in organic vineyards) and years (27%). These findings suggest that bird communities do not impose significant production costs in English vineyards, and that biodiversity conservation is compatible with production. More broadly, our results highlight the importance of distinguishing species presence from functional impacts, and the importance of considering ecological and management impacts when assessing yields.

Highlights

- Bird-mediated grape damage in English vineyards is modest.
- Bird-mediated grape damage is spatially structured and predictable.
- Grape damage by birds is not a driver of yield variation.
- Higher yields are predicted by ecotoxicity arising from agrochemical use.
- Bird conservation in vineyards can be compatible with grape production.

1. Introduction

Biodiversity within agricultural landscapes brings both benefits and costs to production (Zhang et al. 2007), and the relationship between conservation and farming is a complicated one. Agriculture is a key driver of biodiversity decline worldwide (van Klink et al. 2020, Jaureguiberry et al. 2022), yet it is nested within nature, relying on ecosystem services such as pollination and biological pest control (Díaz et al. 2018). Intensive agricultural practices, particularly agrochemical use, accelerate biodiversity declines (Rigal et al. 2023) and, through this, also accelerate the loss of nature's services (Kremen and Merenlender 2018, Tamburini et al. 2020). Incorporating biodiversity-friendly practices and harnessing ecosystem services that enhance production in agricultural landscapes is promoted in policy, for example in Target 10 of the new Global Biodiversity Framework: "*through a substantial increase of the application of biodiversity friendly practices, such as sustainable intensification*, (…) *conserving and restoring biodiversity and maintaining nature's contributions to people, including ecosystem functions and services.*" (Keping 2023). Yet translating these goals into practice is challenging, as biodiversity can also contribute ecosystem disservices (Tschumi et al. 2018, Gonthier et al. 2019, Garcia et al. 2020), such as crop damage, which reduce agricultural productivity. This generates an important question: when balancing services and disservices, how much biodiversity is good for production?

Birds exemplify the dual role of biodiversity in agricultural systems, simultaneously providing ecosystem services and disservices. Importantly, many farmland bird species have undergone rapid population declines, driven largely by land-use change and agricultural intensification (Bowler et al. 2019, Rigal et al. 2023). These declines are likely to alter the magnitude and spatial distribution of bird-mediated services and disservices within crops, yet their consequences for agricultural production remain poorly understood.

In fruit-growing systems, birds can positively contribute to fruit production through biological pest control, where they reduce the populations or activity of insects and vertebrate pests (Jedlicka et al. 2011, Peisley et al. 2015, Barbaro et al. 2017). Biological pest control tends to be higher in more heterogenous landscapes (Barbaro et al. 2017), and its economic value can reach hundreds of dollars per hectare, although it varies across contexts (Garcia et al. 2020). However, the role of birds as biocontrol agents in vineyards remains debated as they are also widely recognised as a source of crop damage through frugivory (Peisley et al. 2015, Denis Thiéry et al. 2018). In extreme cases, bird damage has been reported to reach up to 80% of the crop in Australian and New Zealand vineyards (Tracey and Saunders 2002, Fukuda et al. 2008), and annual losses amounting to millions of dollars have been documented across the United States (Garcia et al. 2020). Rates of frugivory are generally spatially heterogeneous, with higher damage around field edges that neighbour semi-natural habitats (Somers and Morris 2002, Peisley et al. 2017, Adler et al. 2024). As a result, fruit damage is often easily visible whilst pest control services are much less obvious.

Bird-mediated ecosystem services and disservices are affected by both on-farm management and characteristics of the surrounding landscape (Zhang et al. 2007, Pejchar et al. 2018). Homogenous landscapes are associated with reduced pest control and increased frugivory (Rusch et al. 2016, Gonthier et al. 2019, Dainese et al. 2019, Olimpi et al. 2020), whereas landscape complexity and biodiversity-friendly practices can stabilise ecosystem service provision and increase its predictability (Linden et al. 2019, Barbaro et al. 2021, Smith et al. 2022). However, these relationships are context-dependent. For example, pest control by birds may increase yield on conventional but not organic farms (Díaz-Siefer et al. 2022), whilst in some cases, semi-natural habitats can increase ecosystem disservices (Tschumi et al. 2018) and investment in biodiversity-friendly practices can decrease profitability (Scheper et al. 2023). Understanding how bird activity interacts with landscape structure and management to influence yield is therefore crucial for evaluating when biodiversity aligns with, or conflicts with, production goals. However, studies that directly quantify the benefits and costs of animal activity remain rare, particularly in Europe (Peisley et al. 2015), and ecosystem services and disservices are often overlooked in management decisions (Garcia et al. 2020).

Grapes are an important global crop, with over 7 million hectares (5% of the global cover by perennial crops) dedicated to their production (Ritchie and Roser 2013, Venkitasamy et al. 2019). In the UK, viticulture is rapidly expanding (Nesbitt et al. 2019) – since 2005, vineyard hectarage has increased by over 500%, whilst the production in other European countries has been falling (WineGB 2025a). The uptake of biodiversity-friendly management practices is widely promoted and adopted; the industry-led sustainability accreditation scheme 'Sustainable Wines of Great Britain' (hereafter 'SWGB') currently accredits over 40% of UK hectarage (WineGB 2025b). The scheme sets minimum standards for sustainable management and encourages the adoption of 'best practices'. Alongside this, there is increasing adoption of organic management, which covered around 10% of vine hectarage in 2022 (WineGB 2022). Despite this uptake, neither organic nor 'sustainable' vineyard management are presently indicative of consistent biodiversity benefits in English vineyards (Zielonka et al. 2024a) and the industry currently lacks an assessment of how biodiversity contributes to ecosystem services and disservices in these systems. In the absence of clear evidence, management decisions may be shaped more by grower concerns rather than empirical assessments. A recent industry survey identified wasps and birds as the main perceived pest groups (Griffiths-Lee et al. 2022) and concerns over increasing pest pressure have been identified as a barrier to habitat provision and other biodiversity-friendly practices such as hedgerow creation or the promotion of ground vegetation (NBZ pers. comm. 2022).

To address this knowledge gap, we worked across English vineyards spanning gradients of landscape complexity and management practices to assess the effect of birds on grape production. Through grape damage assessments, experimental exclusion of birds and insects, and the relative abundances of service- and disservice- providing bird species as proxies for functionality, our aims were to: (1) quantify the levels of grape damage caused by birds and insects, (2) assess the spatial variation in grape damage, relating it to landscape complexity, vineyard configuration and management practices, (3) examine the relationship between vineyard bird communities and the levels of grape damage, and (4) evaluate the relative importance of birds and management on yield.

2. Methods

2.1. Study system

This study took place across 16 English vineyards (hereafter "sites") spanning the UK's key wine-growing regions (see Zielonka et al. 2024a for full details). The sites were located across southern England (Figure 1), with inter-site distances ranging between 5-300 km and averaging around 100 km. The regional climate is temperate, with growing season temperatures typically ranging between 15–20°C and annual rainfall around 600-800 mm. Global warming is increasing climatic suitability for grape growing (Nesbitt et al. 2022). Vineyards are generally located in lowland areas, ranging from near sea level to 150-200 m elevation, and often planted on south-facing slopes. To ensure viable harvests, all study vineyards had been established for at least three years by 2021.

Fieldwork was conducted in 2021 and in 2022 and aligned with the key stages of the vine lifecycle: 'budding' (early to mid-April), 'flowering' (late June-mid-July), and at 'harvest' (September and October). Each site grew at least two of the four most planted grape varieties in Great Britain (two green varieties: Chardonnay and Bacchus; two red varieties: Pinot Noir and Pinot Meunier), which make up 77% of all plantings in England and Wales (WineGB, 2023).

2.1.1. Landscape and management predictors

Our study sites were chosen to represent the broader English viticultural industry, spanning regions of southern England with highest hectarage of vines (Figure 1) and landscape complexity. The average study vineyard was 21.84 ha ± 5.63 (SE, range 1.14 – 82.1), which is larger than the UK average (6.85 ± 0.6 ha; median: 2.8 ha, n=460 >1 ha; Skelton, 2023) – this is an artefact of our study design as vineyards <1ha were deliberately excluded to enable sufficient sampling at each site. The landscape surrounding sites was characterised using CEH

Land cover 2021 map (Marston et al. 2022) in QGIS (3.30.0). To do this, we summed the proportion of semi-natural habitats (*SNH-cover*; including coniferous and broadleaf woodland and semi-natural grasslands) within a 2.5 km buffer around a centroid of each site. The semi-natural cover around our sites was as low as 1% in highly agricultural landscapes and increased to 42% in heterogenous landscapes. Within each site, vineyards varied in the configuration of fields, with some being composed of a single large field and others being made up of multiple fields interspersed with semi-natural habitats (Figure 1). To capture this variation, we calculated field edge density within each vineyard as a metric of complexity within each site*:*

$$field\ edge\ density\ (m\ ha^{-1}) = \frac{total\ length\ of\ vine\ field\ edges\ (m)}{hectares\ of\ planted\ vines\ per\ site}$$

Vine fields across the sites were bordered by three broad boundary habitat types that may attract different bird species and provide different perching and shelter habitats: open boundaries (lacking habitat features), hedgerows, or woodlands.

Our sites also spanned a management gradient of the English viticultural industry, with six sites being certified-organic, and nine being accredited through SWGB (including one site being accredited through both) and two sites through neither (Appendix A). Here we characterise management intensity according to two measures: *ground vegetation cover* and *ecotoxicity score*. *Ground vegetation cover* was calculated for each site as the mean sward height multiplied by the proportion of ground covered by vegetation in each alleyway. This measure has previously been shown to be higher in vineyards with lower herbicide use and smaller fields, but does not vary significantly based on accreditation status alone (Zielonka et al. 2024a). The *ecotoxicity score* reflected environmental ecotoxicity arising from agrochemicals used at each site. Environmental toxicity data for each active ingredient were obtained from the Pesticide and Bio-pesticide Properties Databases (Lewis et al. 2016), and the resulting active-ingredient ecotoxicity scores were summed for each site, following Möth et al. (2021) and Zielonka et al. 2024(a). The metric has previously been shown to have a significantly negative effect on biodiversity and to be significantly lower in certified-organic than non-organic vineyards, and in non-SWGB than SWGB-accredited vineyards (Zielonka et al. 2024a).

Yield data, recorded as tonnes of grapes harvested per hectare, was collected each study year through a survey completed by vineyard managers. For each site, the manager provided a single yield estimate, which was averaged across fields and grape varieties in a given year at that vineyard.

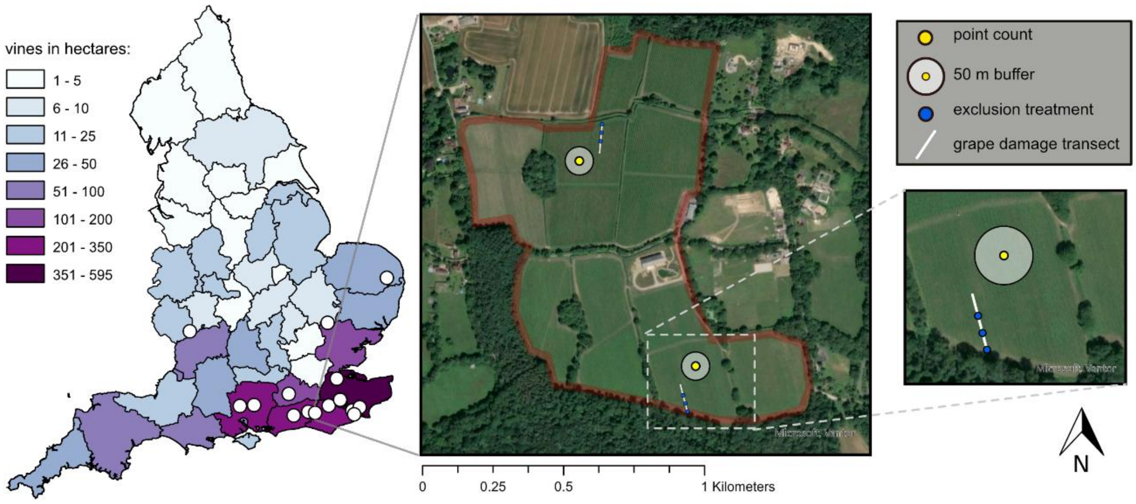

Figure 1. A map of England coloured by the vine hectarage per county with points indicating our 16 sites. Map of one study vineyard is shown, indicating the sampling design across a whole vineyard, and zoomed into one survey field – each survey field had one sampling transect (white lines) along which grape damage was assessed, and where experimental exclusion treatments were deployed (blue points). In each field, we also surveyed birds (yellow points) within a 50 m buffer. In total, we conducted sampling across 28 transects in 16 vineyards.

2.2. Grape damage

Grape damage by birds and insects was quantified in two ways: (i) through grape damage assessments and (ii) an exclusion experiment. Assessments and experimental exclusion were performed in 28 vine fields, each of which was predominantly surrounded by one type of boundary habitat (open n=7, hedgerows n=11 and woodland n=10). On average, there were 1.75 survey vine fields per vineyard (range 1-3 depending on vineyard size; see Appendix A for site level sampling details). One transect, running along a vine row and perpendicular to the field edge, was positioned in each field with the starting point at least 30meters from a field corner to reduce edge effects (Figure 1). Transects varied in length depending on the field size, but all were between 60-100 m. All sampling was undertaken along the same transects, on the same vine plants and by the same observer in both years. Assessments were made within 2 days of the planned harvest of the field in question, which fell across September and October each year.

2.2.1. Grape damage assessments

Grape damage assessments were performed across four most planted grape varieties in England and Wales (WineGB 2023). These were evenly split between white (51.4%) and red (48.6%) grapes. Damage was assessed on three bunches (at around 1 m above the ground) from one vine plant every 10 m along the transect, starting at 0 m. At each bunch, damage was measured as the percentage of the whole bunch that was damaged by birds or insects (Somers & Morris 2002). Bunches showing >50% damage from fungal infections were excluded as assessments of damage by birds or insects would have been unreliable under these circumstances. Damage by birds was characterised by missing grapes (pluck damage, usually caused by larger birds such as Ring-necked pheasants *Phasianus colchicus*), and/or peck damage, which consisted of intact grape skins with some or all pulp and seeds removed (Somers & Morris, 2002, Appendix B). Damage by insects was characterised by small piercings in the grape skin with the juice and pulp sucked out but with the seeds still present (Appendix B). In some cases, it was difficult to reliably determine whether a small bird or an insect initiated the damage as some insects, such as wasps, are known to frequently feed on already damaged grapes, removing more pulp. In these cases, it was assumed that grapes with seeds still present were damaged by insects. In total, 1,509 bunches were assessed across the two years.

2.2.2. Exclusion experiment

The exclusion experiment was performed at the grape bunch scale with three bunches from the same vine plant and at around 1 m above the ground being assigned to either one of the two exclusion treatments (*bird exclusion* and *bird and insect exclusion*) or as a control (Appendix B). The *bird and insect* exclusion was undertaken to better assess bird damage and differentiate it from potential insect damage. Following Nereu et al. (2018), we used green, plastic mesh (mesh size 8 mm) to make the *bird exclusion* bags. For the *bird and insect exclusion* treatment, we fitted an additional insect mesh netting bag (mesh size 1.35 mm) over the green netting bags. The exclusion bags were 40-45 cm in length and 15-20 cm in diameter, which was larger than the expected size of bunches to ensure the bags did not touch the developing grapes.

To ensure sufficient sampling, the experimental treatments were deployed across all of the *grape assessment* transects, as well as some additional ones. In total, the experiment was performed across 46 transects (average 2.88 per site, range 2-5; open boundaries n=12, hedgerows n=19, and woodland n=16; Appendix A), with the treatments being deployed at the grape bunch level at 0, 30 and 60 m away from the field edge (totalling 9 experimental bunches per transect).

The experimental bags were deployed at fruit set (July) and removed at harvest (September / October). During the exclusion experiment, all vineyard activities, including spraying, continued as normal. At harvest, the experimental bunches were assessed for bird and insect damage, following the protocol described above. In 2021, the experimental treatments across two transects were damaged by farming machinery, reducing number of transects to 44. In addition, across the two years, 16 bunches were completely diseased, preventing accurate assessment of damage, and these were excluded. This resulted in 789 experimental bunches used in analyses.

2.3. Bird communities

In each sampling field, bird communities were assessed three times each year (at budding, flowering and harvest) with 10-minute point counts. Bird surveys at harvest were always performed on the same day as grape damage assessments. Point count surveys were conducted between 05:00 – 09:00 and within 3 hours of sunrise, which varied between sampling seasons, and during each survey, all birds seen or heard within a 50 m radius were recorded, excluding birds flying over. Surveys only took place on dry and still days (Bibby et al., 2000), and were performed by the same observer (NBZ).

We characterised all recorded bird species by their diet using the AVONET (Tobias et al. 2022) and SAviTraits 1.0 (Murphy et al. 2023) databases. First, we used the AVONET database to assign each species to their main dietary group: carnivore (including vertivore), invertivore, herbivore (including granivore) or omnivore. Secondly, we used the SAviTraits database to capture variation in species' diets across the three vine-growing seasons, assigning species to season-specific dietary groups based on their predominant food type (see Appendix C). We identified species as 'grape-eaters' if they were observed to feed on ripened grapes by us during fieldwork, or by the vineyard managers, or if they have been previously reported in literature to feed on grapes (e.g. Lamelas-López & Marco, 2021). These species were added to an additional 'grape-eater' group in addition to their main dietary group, which was always either herbivore or omnivore. For each survey in each sampling field, we calculated the total bird abundance, the abundance of birds belonging to each of the four dietary groups (omnivores, carnivores, invertivores, and herbivores), and the abundance of 'grape-eaters'. There was high correlation between total bird abundance and the abundance of grape eaters (R^2=0.830), and so we focused our analyses on the abundance of grape eaters only. One anomaly observation was also omitted from analyses, which included 130 individuals in one survey (second highest number was 96), dominated by a large flock of grape-eating Common starlings *Sturnus vulgaris* (104 individuals; the second highest count of grape-eaters in one survey was 51).

2.4. Statistical analyses

All analyses were conducted in R (version 4.3.0), and general(ised) linear mixed models (GLMMs) were fitted using the *glmmTMB* package (Brooks et al. 2017). We fitted full models and accepted predictor significance if p-value < 0.05. We inspected the distribution of residuals, dispersion, zero inflation and checked for influential points using the *DHARMa* package (Hartig 2022). We also evaluated the random effect structure and compared models with and without random effects using AIC. All response and predictor variables, model structure, error terms and link functions are summarised in Appendix D.

Our analyses focussed on bird damage, which was identified as the dominant source of grape loss, as insect damage was negligible (mean ± SE: 0.83% ± 0.09). We used a hierarchal modelling approach to test the pathway linking landscape structure and vineyard management to bird abundance, grape damage and yield. To ensure consistency and avoid selection bias, we used a common set of predictors that were backed by ecological theory and past research. The included: (i) *semi-natural habitats (SNH) cover*, expected to influence damage through landscape complexity (e.g. Olimpi et al. 2020); (ii) *ground vegetation cover,* which is an important driver of vineyard biodiversity (e.g. Geldenhuys et al. 2021); (iii) *ecotoxicity score*, which varies between management approaches and impacts biodiversity in English vineyards (Zielonka et al. 2024a); and (iv) *field edge density*, which may increase bird access to grapes (Kross et al. 2016, Fontaine et al. 2024). Models also included variables accounting for temporal and spatial variation in sampling.

2.4.1. Spatial and temporal variation in grape damage by birds

To quantify the spatial and temporal variation in grape damage, we modelled the proportion of damaged grapes per bunch using data from grape damage assessment surveys. These results were then validated using data from the experimental exclusion study.

For observational data, the response variable was the proportion of damaged grapes per bunch (0-1), and models were fitted using zero-inflated beta distribution to account for bounded data and excess zeros. Fixed effects included distance from the field edge (0-100m), boundary type (3 levels), year (2 levels) and grape colour (2 levels). For the exclusion experiment, we modelled the proportion of damaged grapes per bunch using a beta-binomial error distribution, specifying the number of damaged and undamaged grapes to account for variation in bunch size and overdispersion. Fixed effects included exclusion treatment (three levels), distance from the field edge (0-60m), boundary type, year and grape colour. Where significant effects of boundary type or exclusion treatment were found, we undertook post-hoc contrast analysis to see which levels significantly varied from each other, using the *emmeans* package (Lenth et al. 2023). All models included nested random effects to account for the sampling design, with transects nested in vineyards. The use of the same vine plant across the study years was accounted for by the fixed effects of experimental exclusion treatment and distance, combined with the random effects.

2.4.2. Relationship between bird communities and grape damage

To investigate the drivers of grape-eating bird abundance and their impact on grape damage, we modelled bird abundance and grape damage in relation to landscape and vineyard management predictors. First, grape-eating bird abundance at harvest was modelled as a function of SNH cover, field edge density, ground vegetation cover, ecotoxicity score and year, using a GLMM with a poisson distribution. Second, to explain variation in damage at the field level, we modelled the mean proportion of damaged grapes per field using a zero-inflated beta distribution. Fixed effects included grape-eating bird abundance, SNH cover, field edge density, ground vegetation cover, ecotoxicity score and year, as well as an interaction between grape eater abundance and field edge density to test whether edge density moderates grape damage by birds by enabling access. Continuous predictors were log-transformed to account for non-linear, diminishing relationships and to improve model fit and convergence. Models included a nested random effect of field ID within vineyard.

2.4.3. Relationship between yield and grape damage

To investigate whether grape damage by birds affected yield, we modelled yield as a function of the mean grape damage per vineyard and key management variables. Yield was related to grape damage, ecotoxicity score, ground vegetation cover and year using GLMMs with a gaussian error distribution. Management predictors, including ecotoxicity score and ground vegetation cover, were included to account for differences in management intensity across sites (e.g. organic and sustainability-certified vineyards). The model included a random effect of vineyard to account for repeated measurements at each site. To further assess the influence of broad management regimes on yield, we compared yield between organic and non-organic, and SWGB-accredited and non-SWGB sites using t-tests.

3. Results

3.1. Grape damage by birds and insects

Bird damage was detected on 24% of surveyed bunches (n=1,509). The mean proportion of damage per bunch was 3.8% ± 0.27 SE, and it decreased significantly with distance away from field edges (slope = -0.006, p-value = 0.010, model R^2 = 0.25; Figure 2A). Damage by birds was significantly higher on red (5.44% ± 0.435) compared to white (1.83% ± 0.248) grapes (z-value = -2.250, p-value = 0.024; Figure 2B). There were no significant differences in bird damage according to boundary type (woodland, hedge or open boundaries), nor between study years (Appendix E).

Results from the exclusion experiment support both overall damage rates and the decline in grape damage with distance from the field edge (Appendix E; Figure 2C). Post hoc comparisons indicated significant differences among all three exclusion treatments. Damage was significantly greater in the control treatment than in the *bird-only* exclusion (estimate = 1.19 ± 0.22 SE, z-value = 5.40, p-value < 0.001) and the combined *bird and insect* exclusion (estimate = 4.81 ± 1.01 SE, z-value = 4.77, p-value < 0.001). Damage was also significantly greater under *bird-only* exclusion than under combined *bird and insect* exclusion (estimate = 3.63 ± 1.02 SE, z-value = 3.56, p-value = 0.001), indicating that insects contributed additional damage when birds were excluded. However, the larger reduction in damage following bird exclusion suggests that birds were the primary source of grape damage (Figure 2C). The exclusion experiment revealed a significant effect of year, with higher damage in 2021 (2.25% ± 0.321) than in 2022 (1.49% ± 0.276; z-value: -2.397, p-value = 0.017).

3.2. Vineyard bird communities and grape damage

In total, we recorded 5,297 birds of 61 species, including 16 species classified as grape-eaters (Appendix C). Total bird abundance was highest at harvest when omnivorous and herbivorous species dominated (Figure 3A). The abundance of grape-eating species was lowest at budding, peaked at harvest, and was significantly higher in 2021 than in 2022 (estimate = -0.247, p-value = 0.002, Figure 3B). Grape-eating bird abundance tended to decline with increasing semi-natural habitat cover, although this relationship was not statistically significant (estimate = -0.244, p-value = 0.058). Abundance did not vary significantly with field edge density, ground vegetation cover or ecotoxicity ($p > 0.05$, Appendix E). It is noteworthy that fixed effects explained a relatively small proportion of the variation in grape-eating species abundance (marginal $R^2 = 0.194$), whereas the inclusion of site identity substantially improved model fit (conditional $R^2 = 0.871$), indicating that site and field-level differences account for a large (~68%) proportion of the variance.

The most abundant grape-eating species at harvest were Common starlings (*Sturnus vulgaris*; 20% of total bird abundance), followed by Common wood pigeons (*Columba palumbus*; 10%), European goldfinches (*Carduelis carduelis*; 9%), Western jackdaws (*Corvus monedula*; 7%), and Ring-necked pheasants (*Phasianus colchicus*; 6%). Across all seasons, we recorded 15 red-listed species (Stanbury et al. 2021), which included seven grape-eating species.

Mean grape damage per field was not significantly related to the abundance of grape-eating bird species (slope = 3.457, p-value = 0.142). However, damage increased significantly with ground vegetation cover (slope = 0.907, p-value < 0.001; Figure 4a) and semi-natural habitats cover (slope = 0.372; p-value = 0.042, Figure 4b). The models also confirmed lower damage in 2022 compared to 2021 (z-value = -3.789; p-value < 0.001; Figure 4c), while no significant effects were detected for ecotoxicity, edge density, or the interaction between bird abundance and edge density (all p-value > 0.05; Appendix E). Fixed effects explained a moderate proportion of the variation in grape damage (marginal R^2 = 0.466), whilst inclusion of site identity substantially improved model fit (conditional R^2 = 0.729), indicating that site-level differences accounted for additional ~26% of the variance.

3.3 Drivers of yield variation

Grape damage by birds did not have a significant effect on yield (slope = -0.076, p-value > 0.05; Figure 5D). Yield increased significantly with ecotoxicity (slope = 0.063, p-value = 0.031, Figure 5A) and was higher in 2022 (4.62 ± 0.47) than in 2021 (3.64 ± 0.38; difference of 27%; estimate = 0.923, p-value = 0.045; Figure 5B). Ground vegetation cover did not significantly affect yield (p-value > 0.05).

Yield was influenced by management type, being lower in certified-organic (3.02 ± 0.78) than non-organic vineyards (4.64 ± 0.37; difference of 53.6%; t-value = 2.982, p-value = 0.006, Figure 5C), and lower in non-SWGB (3.38 ± 0.47) than SWGB-accredited vineyards (4.64 ± 0.37; difference of 37.3%; t-value = -2.449, p-value = 0.039, Figure 5D). All models were validated using simulation-based residual diagnostics. There was no evidence of zero inflation or overdispersion, and model assumptions were adequately met. All model outputs can be found in Appendix E.

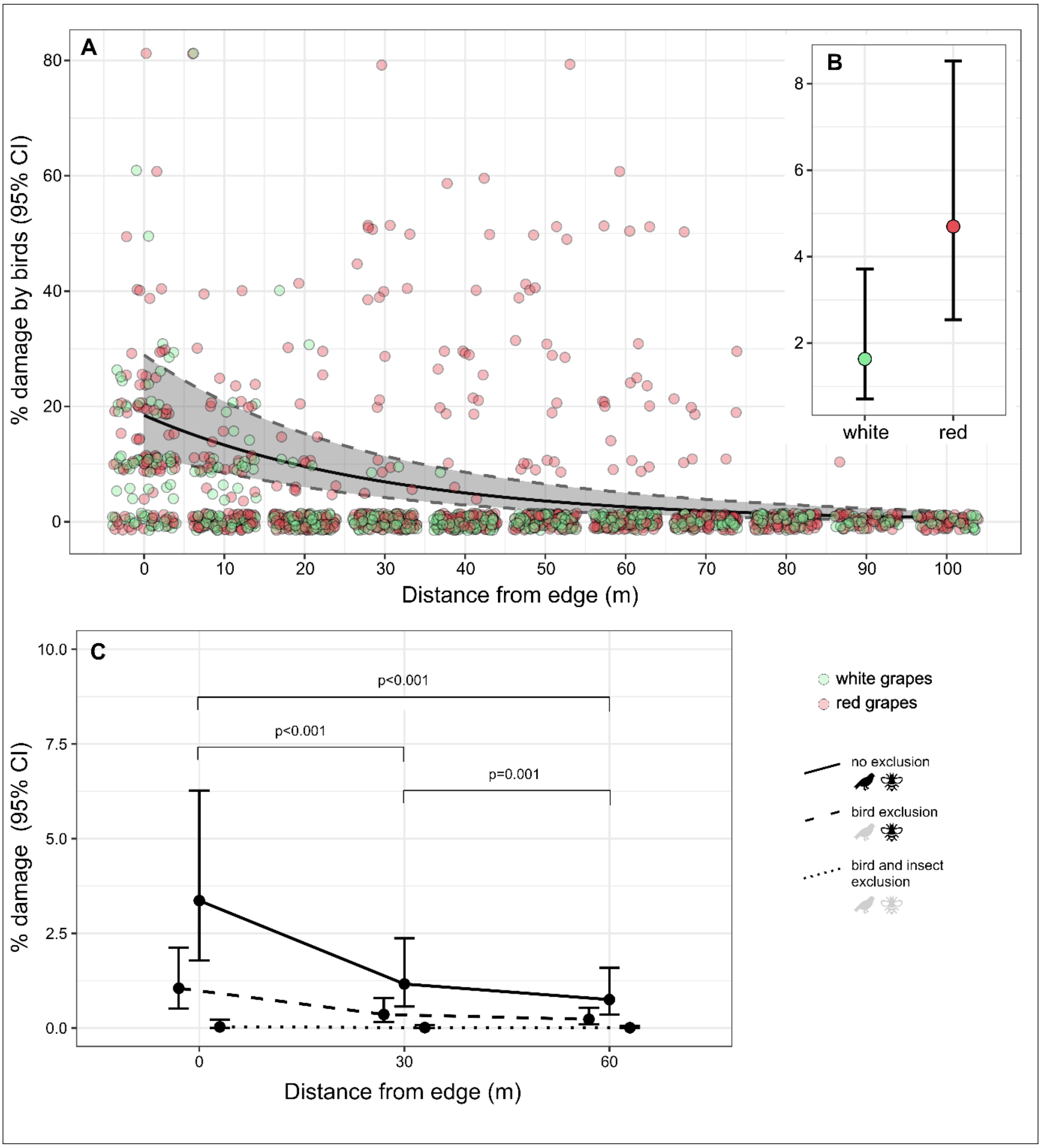

Figure 2. (A) Observed percentage bird-mediated damage per bunches (points) and model-predicted significant relationship with distance from field edge (solid line ± 95% confidence intervals; n=1,509; full model R^2 = 0.25), and the model predicted mean damage (± 95% confidence intervals) by grape colour (B). (C) Model predicted percentage damage to individual bunches (± 95% confidence intervals) under three exclusion treatments at three distances from the edge of a field (0, 30, 60 m; full model R^2 = 0.83). Exclusion treatments

were: *control* (no exclusion), *birds excluded – insect damage only,* and *bird and insects excluded* (n=790 bunches). Grape damage was assessed across 16 vineyards, and damage assessments were performed across 28 transects, whilst the exclusion experiment was performed across 46 transects.

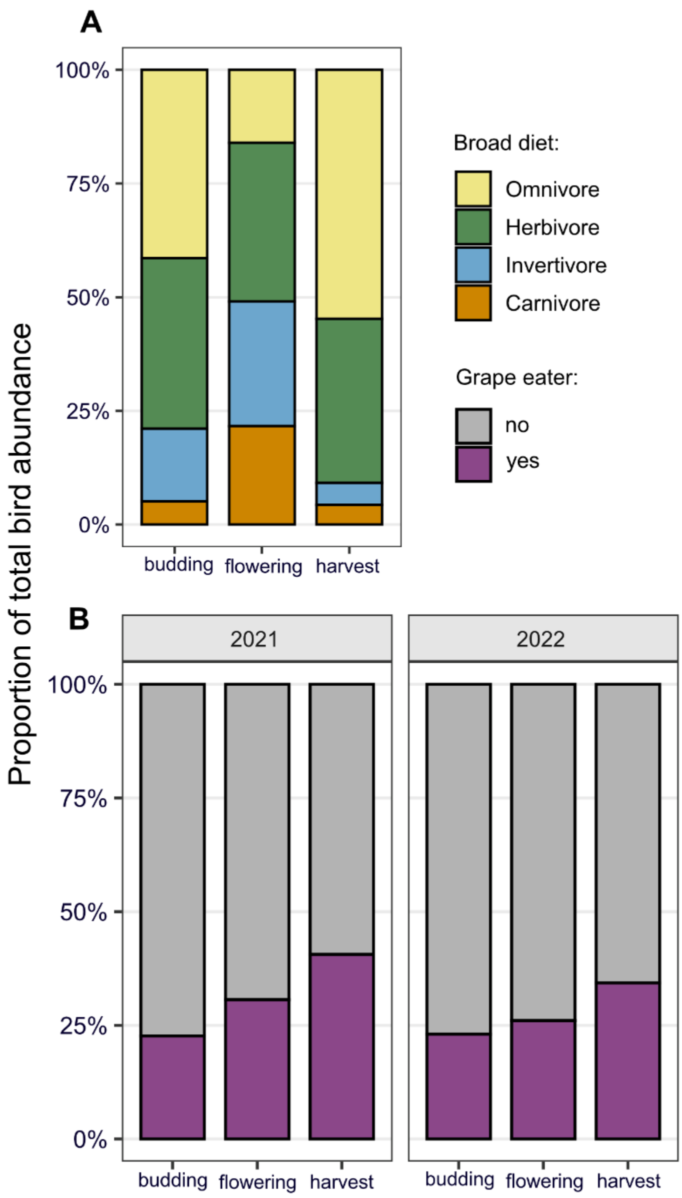

Figure 3. Proportion of individuals belonging to broad diet categories (A; carnivore, herbivore, invertivore, omnivore; B: grape-eating versus non-grape-eating species). Bird community composition is shown across three survey periods (budding, flowering and harvest). The proportion of grape-eating individuals is also compared between the study years (2021 and 2022; p-value = 0.002, full model $R^2 = 0.19$). Bird communities were surveyed in 28 vine fields across 16 vineyards (n = 168 surveys).

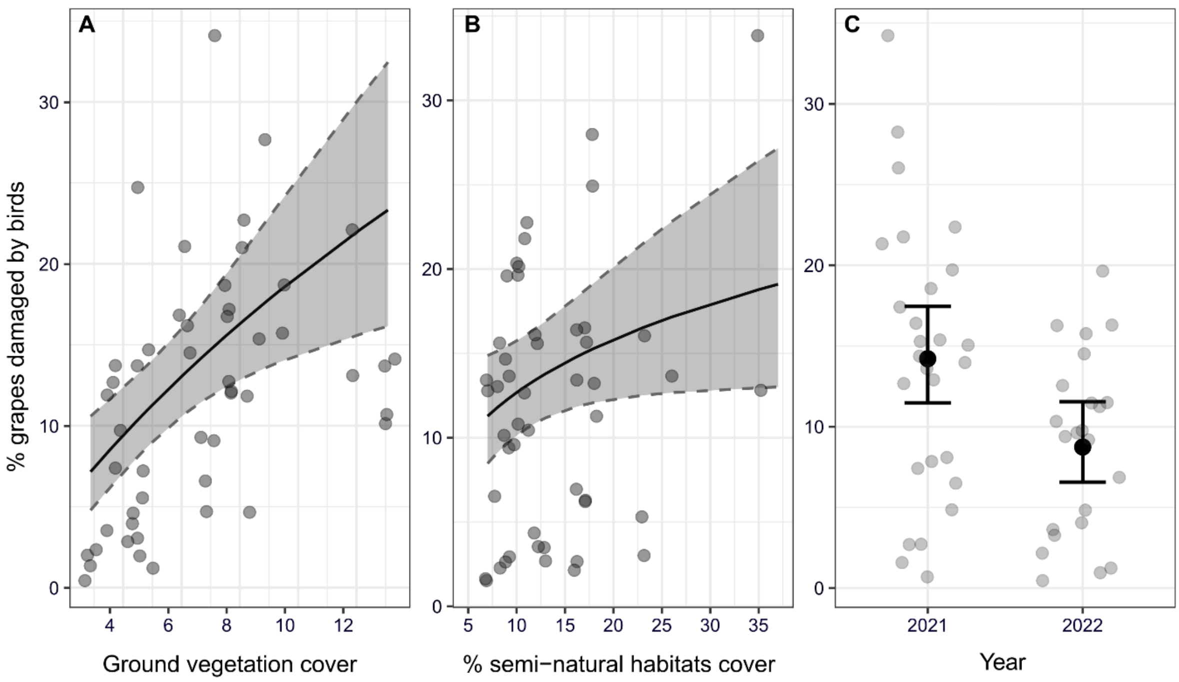

Figure 4. Observed (points) and model-predicted (solid line ± 95% confidence intervals; full model R^2 = 0.57) percentage of grape damage per field in relation to ground vegetation cover (A), percentage cover by semi-natural habitats in the surrounding landscape (B), and study year (C). Grape damage was assessed across 28 fields in 16 English vineyards.

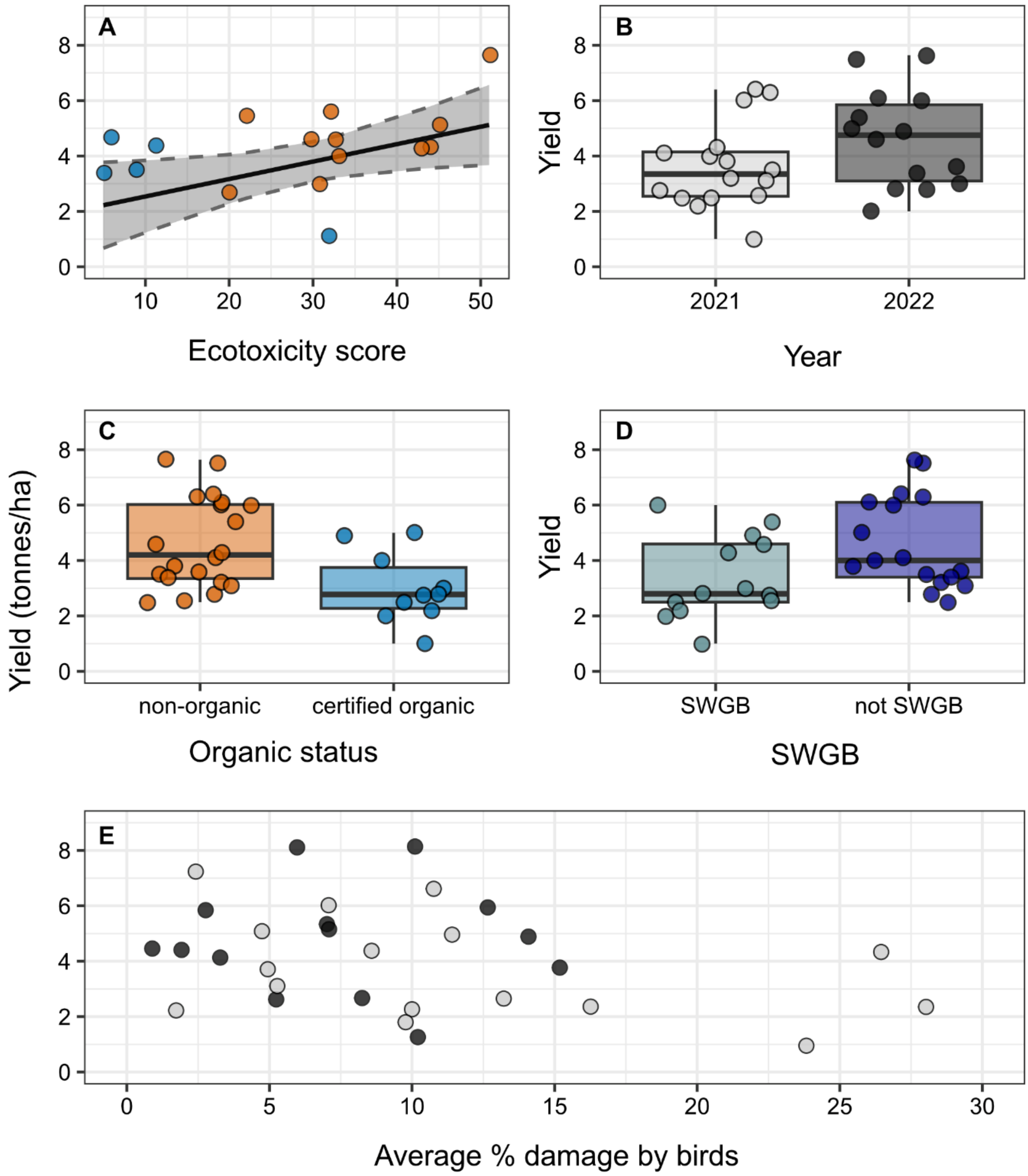

Figure 5. Observed grape yield (points) in relation to the vineyards' ecotoxicity score (A) where points are coloured blue for certified organic and orange for non-organic vineyards; between study years (B); based on vineyards' organic status (C); whether it was accredited through the Sustainable Wines of Great Britain (SWGB) scheme (D); and the non-significant relationship with average grape damage by birds (E) where points are coloured light grey for 2021 and dark

grey for 2022. The model predicted relationship (black line with 95% CI) between yield and ecotoxicity is also shown in A (full model $R^2 = 0.58$). Data comes from 16 English vineyards, of which 6 were certified organic and 10 were SWGB accredited.

4. Discussion

Bird-mediated fruit damage across English vineyards was modest and strongly spatially structured, peaking at field edges. Crucially, damage was not related to the abundance of grape-eating bird species, and instead there was indication of high inter-site and inter-annual variation. We found mixed impacts of semi-natural habitats on damage - whilst damage increased with semi-natural habitat cover in the surrounding landscape and ground vegetation cover within vine fields, there was no effect of wooded edges on the levels of damage. At the same time, variation in yield was driven primarily by management practices and interannual conditions, with no significant effect of bird damage. Together, these results suggest that bird communities do not impose substantial production costs in English vineyards.

4.1. Spatial patterns of grape damage

Bird-mediated grape damage was detected on approximately a quarter of surveyed grape bunches though the direct losses were modest, averaging below 4% damage per bunch. A similarly low level of bird-mediated damage was recently observed in Californian vineyards (~1%; Adler et al. 2024), although higher levels have previously been reported in Australian (8.5%, Peisley et al., 2017), Californian (20%, Kross et al., 2012) and New Zealand (75%, Fukuda et al., 2008) vineyards. Consistent with previous studies (Peisley et al. 2015, Navila Monteagudo et al. 2023, Adler et al. 2024), damage to grape bunches declined sharply with distance from field edges, from around 20% damage per bunch at the edge to 5% at 40 m away from it. This suggests that exposure to edge habitats and easy access to the crop drive frugivory, and is consistent with the idea that edge characteristics can facilitate access to grapes by providing perching places, such as tall trees, and shelter from predators, for example in hedgerows (Somers and Morris 2002, Kross et al. 2012, Peisley et al. 2017, Fontaine et al. 2024). This is supported by our observation of Starlings using telephone wires and electricity pylons within vine fields as perches, allowing birds to feed in the middle of fields rather than only along edges (pers. obs.). This further illustrates the opportunistic nature of bird feeding on grapes.

Bird-mediated damage was significantly higher in red than white grapes, likely reflecting differences in detectability and foraging preferences. Red grapes are more visually conspicuous against green foliage (Melo et al. 2011), and may be preferred due to higher sugar content (Somers and Morris 2002, Fontaine et al. 2024). While grape variety choice was not explicitly tested here, these patterns suggest that planting less conspicuous varieties near vineyard edges could reduce exposure to frugivory.

4.2. Relationship between grape damage and bird communities

Vineyard bird communities were dominated by widespread generalist and omnivorous species, including European starlings, Wood pigeons, and members of the finch and corvid families, all of which have been identified as fruit pests in numerous previous studies (Somers and Morris 2002, Kross et al. 2012, Herrmann and Anderson 2016, Lamelas-López and Marco 2021, Navila Monteagudo et al. 2023). Despite this, we found no relationship between bird abundance and grape damage, highlighting the need for caution when inferring impact from species presence alone. Previous studies have shown that grape-eating behaviour, though not abundance *per se,* can be reduced in the presence of predatory species (Kross et al. 2012), and that some species may simultaneously contribute both ecosystem services (e.g. pest control) and disservices through frugivory (Kross et al. 2016, Garcia et al. 2020). This suggests that the impact of birds, and frugivory, may be context-dependent and driven by behaviour rather than overall abundance.

Opportunistic frugivory is likely to vary interannually depending on the availability of alternative food resources in the surrounding landscape and the timing of grape ripening. In our study, evidence of year effects on frugivory was mixed. While observational damage did not differ significantly between years, the exclusion experiment and averaged field-level estimates indicated lower damage in 2022. This year was also characterised by lower abundance of grape-eating species and a later harvest, when there may have been higher availability of fruits in the wider landscape, and therefore lower foraging pressure (Herrmann and Anderson 2016, Lindell et al. 2018), and potentially alter the likelihood of birds exploiting vineyards. These findings suggest that grape damage is at least partially shaped by interannual variation in phenology and resource availability, making it difficult to predict. This temporal variability may become increasingly important under climate change, which is expected to alter both fruiting phenology and bird foraging behaviour (Llanaj and McGregor 2022).

Notably, grape damage increased with semi-natural habitat cover in the wider landscape and ground vegetation cover, yet showed no relationship with the presence of wooded edges, such as hedges and woodlands. Conversely, grape-eating bird abundance tended to decline with increasing semi-natural habitat cover, albeit this relationship was only marginally significant ($p=0.058$). Thus, the positive association between semi-natural habitat cover and grape damage does not appear to result simply from a greater abundance of grape-eating birds. Rather, these results suggest that damage is not driven by the presence of semi-natural habitats *per se,* but by how habitat structure influences access to grapes and the behaviour of a subset of species. Semi-natural habitats and ground vegetation likely provide foraging resources, shelter and movement corridors, and have been shown to support bird communities in vineyards (Kross et al. 2016, Adler et al. 2024, Fontaine et al. 2024, Rösch et al. 2024). However, this does not necessarily translate to increased abundance of grape-eating species at the field scale, with our results suggesting, if anything, a decline in their abundance with increasing semi-natural habitat cover. This suggests that vineyards do not act as strong attractors that restructure bird communities at the landscape scale (Herrmann and Anderson 2016, Zielonka et al. 2024a), and that frugivory occurs opportunistically. This interpretation is further supported by the strong contribution of site-level random effects in our models, indicating that a substantial proportion of variation in damage is driven by unmeasured, site-specific factors. Together, these findings suggest that grape damage is context-dependent and difficult to predict based on bird abundance or broad habitat metrics alone.

4.3. Yield variation

Bird-mediated grape damage was not a driver of yield across English vineyards. Instead, yield variation was explained by management and inter-annual conditions. Yields were significantly lower in organic (-53%) compared to non-organic vineyards, and higher in vineyards accredited through the Sustainable Wines of Great Britain (SWGB) scheme (+37%) than in non-SWGB vineyards. This aligns with earlier research reporting lower yields in organically managed systems (Döring et al., 2015; Seufert et al., 2012), and may be linked to differences in agrochemical inputs, as reflected by the positive relationship between vineyard ecotoxicity scores and yield. These differences may also be exacerbated by challenges in disease control under organic management (Samnegård et al. 2019), where pathogens such as downy mildew and *Botrytis* can cause substantial yield losses (Griffiths-Lee et al. 2022). Effective management of diseases may be an important driver of yield variation and likely underpins much of the observed yield gap between management systems.

Interannual variation in yield was substantial (27%), reflecting the sensitivity of grape production to climatic conditions. Frost events during bud development and periods of extreme heat can have lasting effects on fruit development, quality and disease susceptibility, particularly of *Botrytis* (Camps and Ramos 2012, Llanaj and McGregor 2022), further complicating predictions of yield outcomes.

4.4. Limitations and future research

Several limitations should be considered when interpreting these results. First, we did not record bird behaviour to empirically measure grape-eating activity. Instead, we analysed the relationship between the abundance of grape-eating birds and grape damage, using reports from vineyard managers and earlier research from other systems to classify species as grape-eaters. Our results highlight the limitations of this approach, as Common starlings were the most abundant grape-eating species in our dataset, but their numbers were not directly linked to increased damage. Making extrapolations from broad diet categories is also problematic, as earlier research has observed largely insectivorous species that are strongly associated with woodlands occasionally moving into vineyards to feed on grapes (Adler et al. 2024). In addition, a small number of species or individuals may contribute disproportionately to damage, which may be better explained by traits such as body size and foraging strategy, rather than abundance alone. Future studies incorporating direct observations or camera-based approaches (e.g. Fontaine et al. 2024) could quantify species-specific impacts and better link bird communities with functional outcomes.

Our approach to relating bird communities, grape damage and yield is also simplistic and may have missed some key pathways. First, we did not directly measure other services (such as pest control or disruption of disease transmission) or disservices (increased spread of pathogens, bud damage) that could be provided by birds in vineyards. In vineyards, insects can act as vectors of grapevine pathogens, meaning that bird predation on insects could reduce disease transmission (Favor et al. 2024, Dara et al. 2025). At the same time, damage to grape skins caused by birds can create entry points for pathogens and increase grapevine's susceptibility to bunch rot. Bird can also reduce yields by consuming and damaging buds earlier in the season (Hollinshead et al. 2024). As such, birds may simultaneously have positive and negative impacts on grape health and yield that were not fully captured in this study.

Lastly, several caveats to our sampling design should be acknowledged. Our estimates of bird abundance did not explicitly account for imperfect detection, which may vary among species, habitats, and survey conditions. Whilst our study design did not allow us to model detection we expect its impact on abundance estimates to be low because all surveys were conducted on dry days without strong winds, by the same observer, only during early mornings and all sites were similar in structure. In a similar vein, our measures of habitat structure were relatively coarse and may not capture fine-scale features influencing bird movement and foraging, such as perch availability or vegetation configuration within fields. Strong site-level random effects suggest that unmeasured local factors could be shaping bird communities, foraging behaviour and damage outcomes. Future work could incorporate repeated surveys to better account for detection differences and to resolve finer-scale drivers of bird abundance and foraging. Together, these limitations highlight the complexity and context-dependence of bird-mediated effects in vineyards and the need for further studies that consider ecological and management variables.

4.5. *Applications and conservation recommendations*

Managing bird damage is often perceived as a challenge among vineyard managers and raises legitimate conservation concerns. However, our results indicate that broad-scale exclusion or management of birds is rarely necessary. Several grape-eating species are nationally red-listed and have undergone substantial population declines, meaning that deterrence measures must be applied with caution. For example, Common starling populations have declined by 57% across the UK since 1995 (Stanbury et al. 2021). Nevertheless, as a gregarious species, they can appear locally in large numbers, resulting in episodic and visually conspicuous grape damage. In addition, short-term exclusion of birds through netting and deterrents are often labour intensive, costly, raise sustainability concerns (Tracey and Saunders 2002, Wang et al. 2020, Bouvier et al. 2022), and may negatively affect the aesthetic and recreational value of vineyards.

Targeted management focussing on vineyard edges or key damaging species is likely to be more cost-effective. With improved understanding of the functional roles of birds in English vineyards, context-specific recommendations could be made. For instance, nest boxes may promote non-grape eating insectivorous species that limit insect damage and disease spread, without contributing to crop damage (Jedlicka et al. 2011, Lindell et al. 2018), whilst predatory bird species could be encouraged to reduce frugivory (Kross et al. 2012, Peisley et al. 2017). Simple design considerations, such as avoiding planting vines directly beneath pylons or other elevated perching structures, may also help limit bird access to grapes. Importantly, management responses should consider local context. For example, Ring-necked Pheasants are known grape-eaters and they can reach artificially high local abundances around grape harvest due to releases for game shooting in England, presenting a human-induced source of conflict that may be beyond the control of vineyard managers.

The positive association between grape damage and semi-natural habitats and ground vegetation should not be interpreted as evidence that these features are detrimental. A large body of literature demonstrates that such habitats support biodiversity and ecosystem services in vineyards (Duarte et al. 2014, Geldenhuys et al. 2021, Griffiths-Lee et al. 2022, Zielonka et al. 2024a). As such, removing these habitats would likely be detrimental to biodiversity and could risk the loss of ecosystem functions. Instead, spatial configuration may be important to consider: for example, wider grassland margins could act as buffers between edge habitats and the vine rows, potentially reducing frugivory and supporting biodiversity.

Industry-led sustainability schemes, such as Sustainable Wines of Great Britain, are well placed to promote approaches that help reconcile production with conservation goals by encouraging habitat retention and landscape heterogeneity. They may also support growers through incentives that offset modest yield losses. Beyond production, conserving bird communities can provide cultural, wellbeing and economic benefits (Whelan et al. 2015, Winkler and Nicholas 2016, Assandri et al. 2018). In a parallel study, we found that higher bird species richness enhanced vineyard soundscapes and visitor experience during vineyard tours (Zielonka et al. 2024b). This is an important consideration as vineyard tourism contributes around a quarter of total revenue across the UK viticultural industry (WineGB 2023) and many vineyards are embedded within wider recreational landscapes, including national walking routes. Given the modest and spatially predictable nature of bird-mediated grape damage observed here, these findings suggest that embracing limited crop losses may be outweighed by gains in visitor experience and landscape perceptions by local communities. Together, this reinforces the value of birds as multifunctional contributors to viticultural landscapes, highlighting the importance of considering wider societal outcomes in sustainable agriculture business models.

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Author contributions

Fill out during submission based on the available categories.

Conflict of Interest Statement

Authors declare no conflict of interest.

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