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RESEARCH ARTICLE

Forest cover enhances pest control by birds and bats independently of vineyard management intensity

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Abstract

1. Agricultural intensification substantially threatens farmland communities and associated ecosystem services. More specifically, landscape simplification and agrochemical use can significantly alter the activity of natural enemies, contributing to hampered pest suppression. At the same time, the effects of these factors on vertebrate predators and their contribution to pest control are relatively understudied, especially in European permanent crops.
2. Using exclosures in Hungarian vineyards, we investigated the effect of birds and bats on arthropods affecting ecosystem functions and crop yield considering the local management (organic vs. integrated pest management [IPM]) and contrasting landscape heterogeneity of the plantations. We also collected abundance data of the European grapevine moth (*Lobesia botrana*) and canopy-dwelling herbivorous and predatory arthropods and quantified fruit and leaf damage and sentinel prey predation associated with these groups.
3. As opposed to summer bat activity, forested and connected landscapes promoted high insectivorous bird abundance and bat activity in spring and contributed to lower fruit damage caused by *L. botrana*. Vineyard management showed no effect on birds and bats. In contrast, canopy-dwelling arthropod density was higher in organic than in IPM vineyards, resulting in higher leaf herbivory and the occurrence of caterpillar predation there.
4. Bird and bat exclusion increased leaf herbivory and fruit damage, leading to higher yields in control plots. Furthermore, increased bat activity significantly decreased the abundance of the major grape pest, *L. botrana*, in spring.
5. *Synthesis and applications*. Our results highlight the importance of bats and birds in reducing herbivory and increasing economic benefits in vineyards. Their presence

and foraging activity can be promoted by connected landscapes incorporating hedgerows and small groups of trees as well as native, deciduous forest patches that can potentially increase the amount of food sources and suitable nesting and roosting sites. Organic vineyards in these landscapes can further enhance pest control services by supporting predatory arthropods.

KEYWORDS
biocontrol, cage experiment, ecosystem services, herbivory, landscape, management, natural enemies, predation

1 | INTRODUCTION

The general trend of agricultural expansion and land use intensification observed in the past decades to meet growing human needs is still ongoing worldwide (Rudel et al., 2009). This process is associated with the transformation of natural and semi-natural landscapes into agricultural areas and the intensive use of agrochemical inputs, contributing to taxonomically and functionally impoverished farming communities (Batáry et al., 2020). Therefore, recent studies have highlighted an urgent need to develop strategies for enhancing ecological intensification to maintain ecosystem processes and services in agricultural areas and to achieve sustainable production (Kleijn et al., 2019; Rader et al., 2024).

Vineyards are significant cultural, ecological and economic systems, covering about 7.2 million hectares worldwide, of which about 50% are concentrated in Europe (OIV, 2023). This coverage is expected to expand due to the high demand for related provisioning and cultural services, as well as the increasing availability of exploitable areas at the cooler boundary of the potential vine range due to climate change (Candiago et al., 2023). Vineyards face numerous pests and diseases, and despite improving trends, only relatively small areas adopt sustainable management practices (e.g. only 12% of European vineyards are organic) (ECA, 2023). Most vineyards still rely heavily on pesticide treatments, which adversely affect non-targeted organisms (Provost & Pedneault, 2016). For example, the European grapevine moth (*Lobesia botrana*), a widespread and significant grape pest causing severe damage and yield loss, is primarily managed by synthetic insecticides, hampering the regulation by natural enemies (Thiéry et al., 2018). However, under suitable conditions, vineyards have the potential to offer effective pest control services by fostering diverse and abundant predator communities, such as birds, bats, and arthropods (Charbonnier et al., 2021; Lourenço et al., 2021; Pertot et al., 2017).

Natural pest control provided by a wide range of vertebrate and invertebrate taxa is one of the most important ecosystem services in agrosystems (Begg et al., 2017; Jonsson et al., 2014), with an estimated economic value of US$ 417 per ha and year across biomes (Sheng et al., 2024). Among various taxonomic groups, birds and bats are key components of biodiversity-based ecosystem services and are considered significant pest suppression agents (Herrera et al., 2021; Maas et al., 2016). For instance, farmland birds consume about 28 million tons of prey per year, including large numbers of herbivorous insects (Nyffeler et al., 2018), and bats consume over 70% of their body mass in arthropods each night, including more than 700 identified pest species in their diet (Tuneu-Corral et al., 2023). At the same time, particularly birds can contribute to some disservices like dampened strength of trophic cascades through feeding on predatory arthropods (Maas et al., 2016; Monteagudo et al., 2023; Thiéry et al., 2018).

The effectiveness of these services (or disservices) strongly depends on factors at different spatial scales (Tscharntke et al., 2016). Contrary to conventional crop protection practices, through an increased amount of food resources associated with the release of pesticides, organic farming promotes a broad spectrum of ecological functions and a high proportion of vertebrate species with pest control importance (Ancillotto et al., 2023; Barbaro et al., 2021; Wickramasinghe et al., 2004; Winqvist et al., 2012). Another influencing factor is the landscape context, which might be of greater importance than the local features of agricultural areas alone (Tscharntke et al., 2021). For instance, the increasing amount and connectivity of natural non-crop habitats in the surrounding landscape are crucial for vineyard biodiversity (Paiola et al., 2020) and positively affect the composition and activity of bat communities (Costa et al., 2020; Frey-Ehrenbold et al., 2013) and promote greater richness and density of insectivorous birds (Endenburg et al., 2019; Lourenço et al., 2021).

Experimental exclosure constitutes a powerful tool for identifying complex interactions between vertebrates and invertebrates affecting ecosystem services and crop yield. However, previous results have been primarily reported from tropical areas (Maas et al., 2019; Tuneu-Corral et al., 2023), and such studies on European permanent agrosystems are still scarce (Ancillotto et al., 2024). Although birds and bats are commonly targeted by conservation measures, some farmers still tend to invest less effort in attracting them, neglecting the pest control services these animals can provide (Kross et al., 2018). In this study, we conducted an exclosure experiment in Hungarian vineyards with distinct management practices and landscape characteristics to investigate the role of birds and bats in shaping arthropod density patterns and associated ecosystem functions. We had the following hypotheses: (1) organic vineyard management and forested landscapes increase the abundance and activity of birds and bats; (2) a higher number and activity of birds and bats result in a decreased abundance of pest insects, and also (3) reduced insect herbivory and increased crop yield, but hampered predation pressure by arthropods.

2 | MATERIALS AND METHODS

2.1 | Study area and design

We conducted our study in the western part of the Transdanubian Mountains (Tapolca Basin and Balaton Uplands) and the southern part of the Little Hungarian Plain (Marcal Basin), Hungary (Figure S1). This region is characterized by a continental climate with sub-Mediterranean influence and a mean annual temperature of 9–11°C and precipitation of 550–650 mm (Mezősi, 2017). For the experiment, we selected 12 vineyards (including 10 grape varieties; one or two varieties per plantation), six with organic management, and another six with integrated pest management (IPM). In contrast to IPM vineyards, organic vineyards (3.2% of the Hungarian vineyards; HSCO, 2025) were managed without any herbicide, synthetic insecticide and fertilizer applications and had generally smaller area and yield, and higher herbaceous vegetation in our study area (Table S1). For IPM vineyards, limited chemical inputs are targeted based on pest monitoring to maintain their populations below crop injury levels (Paredes et al., 2021).

Vineyard landscapes were classified as 'forested' and 'non-forested' according to their composition and configuration within 500 and 1000 m radius buffers based on CORINE Land Cover (Copernicus Land Monitoring Service, 2018), the Ecosystem Map of Hungary (Tanács et al., 2021) and Google satellite images (taken in 2023) using the QGIS 3.6.1 (QGIS Development Team, 2019) and Conefor Sensinode 2.6 software (Saura & Torné, 2009). At both spatial scales, forested landscapes had the highest share of deciduous forests and the greatest connectivity of woody elements (i.e. forest patches, hedgerows, large groups of trees), whereas non-forested landscapes had a relatively large proportion of arable lands and the greatest vineyard-forest distances (Table S2). Altogether, we had three replications of vineyards for each factor combination (i.e. organic and forested, organic and non-forested, IPM and forested, IPM and non-forested). The distance between vineyards was between 1 and 38 km (mean ± SE: 16.7 ± 1.7).

We established two control and complete exclosure plot pairs ($n = 24$; altogether 48 plots) in the centre of each vineyard at least 100 m apart and 25 m from the edge. For each plot pair, the control and exclusion plots were 25 m apart (Figure 1a). The cages for exclosure plots consisted of rectangular wire cables connected by bamboo poles and fully covered with openable agricultural netting (mesh size of 2.5 × 2.5 cm) that ensured the insects' access (including moths) to the crop plants but did not allow birds and bats to reach the canopy. An exclosure cage was 6 × 0.7 × 2 m (length × width × height) in size, always covering six grapevine plants (Figure S2). We installed the cages in the first half of April 2023, removed them at the end of August 2023 before the harvest, and maintained them regularly during the study period. Within each vineyard, control and excluded grapevines were cultivated similarly (e.g. mowing, pruning, shoot training and trimming).

2.2 | Data collection

We used the point count method (5 min per observation point, $r = 50$ m) for bird observations (Bibby et al., 2000) and designated bird observation points ($n = 24$) for each plot pair between the control and exclusion plots (Figure 1a). We surveyed birds twice during the main breeding period (i.e. with the highest detectability) with the first survey conducted between May 2–4 and the second between May 15–17. We further classified bird species into functional insectivores, that is, birds that are insectivorous in the breeding period and mainly forage on leaves or hunt in flight (Brambilla & Gatti, 2022).

For bat surveys, we conducted acoustic samplings between 17–19 May and 12–14 July for 5 h during three consecutive nights, starting 30 min before sunset. We installed AudioMoth full-spectrum acoustic devices ($n = 24$) to record bat calls (Hill et al., 2018) at the locations used for bird observations (Figure 1a). The average temperature of the sampling locations was 15.9 ± 0.2 (mean ± SE) in May and 27.2 ± 0.2 in July. For bat call recordings, the sampling frequency was 256 kHz; the gain was set to medium; the recording chunks were 295 s long with 5 s sleep to save the files (Szabadi et al., 2023). We searched bat calls automatically using the Bat Detective program (Mac Aodha et al., 2018) and cut out the sequences from the recordings using a self-written script in the R 4.4.2 statistical environment (R Core Team, 2024). We defined a sequence as a series of echolocation calls with an inter-pulse interval between calls of less than 3 s. Finally, we manually validated the automatic species-level identifications of sequences in the Kaleidoscope Pro software (Wildlife Acoustics, Inc.) and defined bat activity as the number of 5 s intervals containing bat calls.

We used specific pheromone baited traps (CSALOMON® RAG, Plant Protection Institute, Hungary) to collect *Lobesia botrana* individuals. We installed the traps at canopy level, close to the bird and bat observation points ($n = 24$, Figure 1a), and collected moths for 7 days on three occasions between 15–21 May, 10–16 July and 21–27 August. Within the same periods, we collected canopy-dwelling arthropods with beating and D-Vac sampling methods (Basset et al., 1997) from the odd-numbered plants (1, 3, 5) within each plot (Figure 1b). The materials of the two sampling methods and three plants within each plot were handled together ($n = 48$). We counted and identified the individuals to the lowest taxonomic level where the classification by functional group (i.e. herbivores and predators) was possible.

We measured leaf herbivory, fruit damage, and predation on the even-numbered plants (2, 4, 6) of each plot (Figure 1b). We assessed grape berry damage by arthropods, primarily the perforations of *L. botrana* larvae, by calculating the proportion of damaged berries for

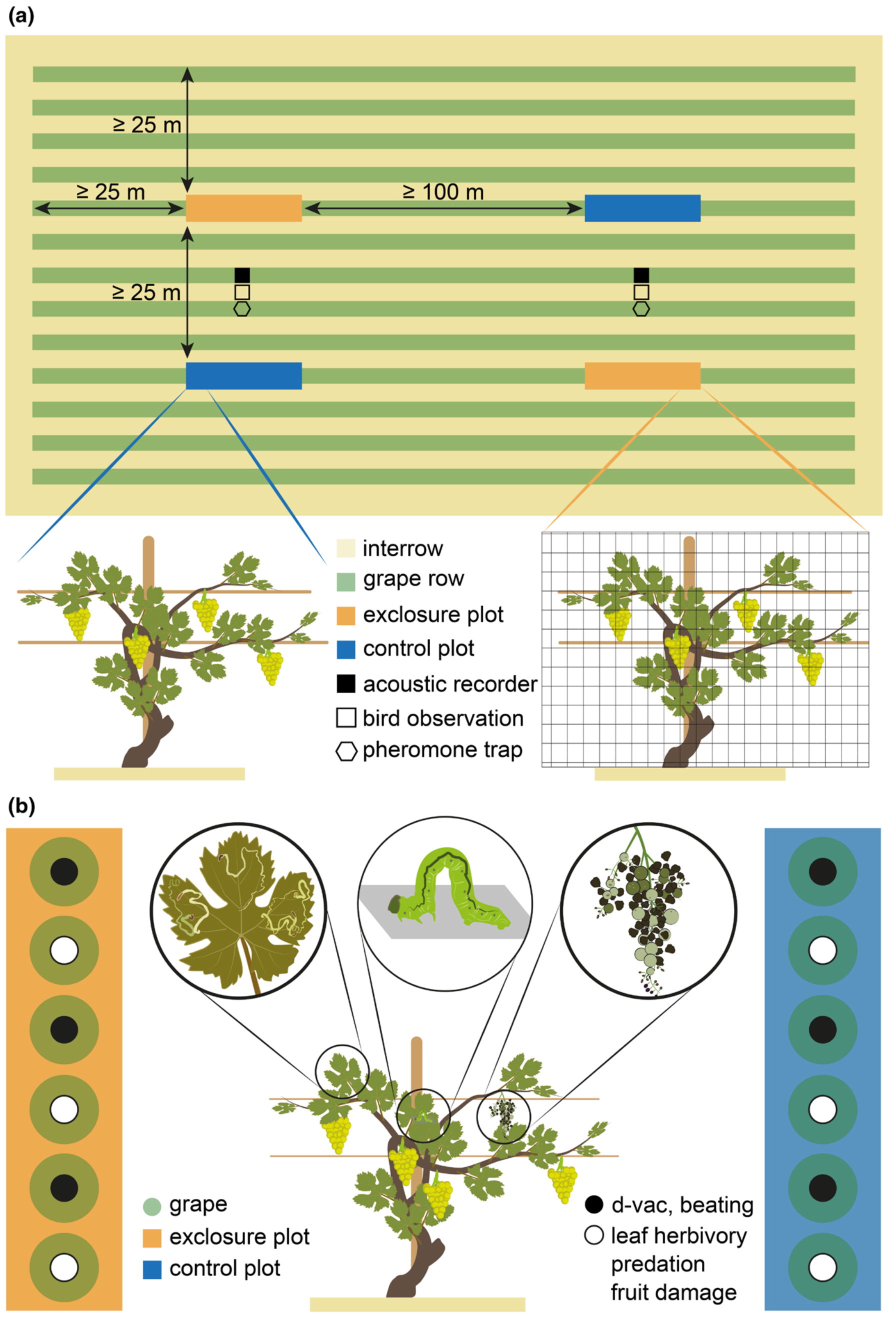

FIGURE 1 (a) Spatial arrangement of plots, bat acoustic recorders, bird observation points and pheromone traps within vineyards; (b) grape plants used for arthropod sampling and leaf herbivory, fruit damage and predation measurements within plots.

five randomly selected clusters per plant ($n = 48 \times 3 \times 5 = 720$) before the harvest and cage removal in late August. Simultaneously, we visually inspected leaf herbivory on ten randomly chosen leaves per plant ($n = 48 \times 3 \times 10 = 1440$) and calculated the proportion of damaged surfaces caused by herbivorous insects. We investigated the predation by arthropods with a sentinel prey experiment in mid-May. We fixed the dummy caterpillars to five randomly selected leaves per plant ($n = 48 \times 3 \times 5 = 720$) and exposed them for 7 days for subsequent inspection of predation marks in the laboratory. For further details on bird observations, arthropod collections, and sentinel prey, see Supplementary Methods section (Data collection) of Supporting Information. Fieldwork was conducted in agreement with the vineyard owners, and no specific permissions or ethical approvals were required for data collection.

2.3 | Data analysis

We created four groups of generalized linear mixed-effects models to test the effect of (1) local vineyard management (organic vs. IPM), landscape (forested vs. non-forested), and their interaction on overall and insectivorous bird abundance as well as overall and seasonal (spring and summer) bat activities; (2) management, forest proximity and treatment (control vs. exclusion; except moths) and their interactions on overall and temporal moth and overall canopy-dwelling arthropod abundances; (3) management, forest proximity, treatment, and their interactions on leaf herbivory, fruit damage and occurrence of predation; and (4) to test functional relationships, that is (a) the effects of bird abundance and bat activity on overall canopy-dwelling arthropod as well as overall and temporal (May and July) moth abundances, and (b) the effect of moth abundance on fruit damage. For the structure of the full models and included random terms, see Table S3.

We used the R 4.4.2 statistical environment for all analyses. Models were fitted using 'glmer' (Poisson regression: bird and canopy-dwelling arthropod abundances; binomial regression: occurrence of predation) and 'glmer.nb' functions (negative-binomial regression: bat activities and moth abundances) of 'lme4' package (Bates et al., 2015), and 'glmmTMB' function (ordered beta regression: leaf herbivory and fruit damage) of 'glmmTMB' package (Brooks et al., 2017). We conducted an Akaike Information Criterion (AICc)-based automatic model selection using the 'MuMIn' package (Bartoń, 2024) and applied model averaging for models with a ΔAICc <2. The models were tested using type II Wald χ^2 tests using the function 'Anova' of 'car' package (Fox & Weisberg, 2019). For details on data preparation for the analyses, see Supplementary Methods section (Data preparation) of Supporting Information.

2.4 | Yield calculations

To determine the role of birds and bats in influencing crop yield, we followed the methodology used by Rodríguez-San Pedro et al. (2020). First, we calculated the difference between the overall average percentages of damaged berries observed in control and exclusion plots (for the same clusters used for grape berry damage analyses). Then, we calculated the average yield (kg/ha) considering data for the studied vineyards obtained directly from the owners. Finally, we multiplied this averaged yield value by the difference in average grape berry damage between the treatments.

3 | RESULTS

We observed 1068 birds belonging to 50 species, of which 265 individuals of 17 species were functional insectivores (Table S5) and recorded 3412 bat passes representing nine identified taxa (Table S6). The analysis of overall bird abundance and bat activity showed no significant effects from any of the variables. However, we found a significant landscape effect on insectivorous birds, with higher numbers in vineyards in forested compared to those situated in non-forested landscapes (+50%, $\chi^2 = 10.456$, $p = 0.001$; Figure 2a). In addition, bat activity in spring was higher in vineyards in forested than non-forested landscapes (+127%, $\chi^2 = 7.340$, $p = 0.007$; Figure 2b), while their activity in summer was higher in vineyards situated in non-forested landscapes (+124%, $\chi^2 = 7.612$, $p = 0.006$; Figure 2c). The vineyard management had no significant effect on bird densities and bat activities (Table S4).

We collected 3601 *Lobesia botrana*, 256 canopy-dwelling herbivorous and 396 predatory arthropod individuals (Tables S7 and S8). We found no significant management and landscape effects on *L. botrana* abundance, except in August, when it was significantly higher in IPM than in organic vineyards (+165.9%, $\chi^2 = 4.823$, $p = 0.028$; Figure 3a). Vineyard management significantly affected canopy-dwelling arthropod abundance as there were more herbivorous and predatory arthropods in organic than in IPM vineyards (herbivores: +124.1%, $\chi^2 = 10.329$, $p = 0.001$; predators: +130%, $\chi^2 = 34.432$, $p = 0.000$; Figure 3b,c). Canopy-dwelling arthropod densities were unaffected by forest proximity and treatment (Table S4).

Average fruit damage was significantly higher in vineyards situated in non-forested than in forested landscapes (2.1% difference, $\chi^2 = 7.069$, $p = 0.008$; Figure 4a) and also in exclusion plots, where natural enemies had no access to plants, compared to control plots ($\chi^2 = 8.905$, $p = 0.003$; Figure 4b). Exclosure plots had 3.4% of grape berries damaged compared to 2.2% recorded in control plots resulting in a 1.2% difference, that is, the proportion of damaged berries increased by 54.5% with exclusion. In our studied vineyards, the yield was, on average, 6085.4 kg/ha (IPM: 8750; organic: 3420.8). Considering these values, we estimated that bird and bat exclusion reduced the yield by 73.1 kg/ha on average (IPM: 105; organic: 41.1). We found a significant interacting effect of the management and treatment on leaf herbivory as it

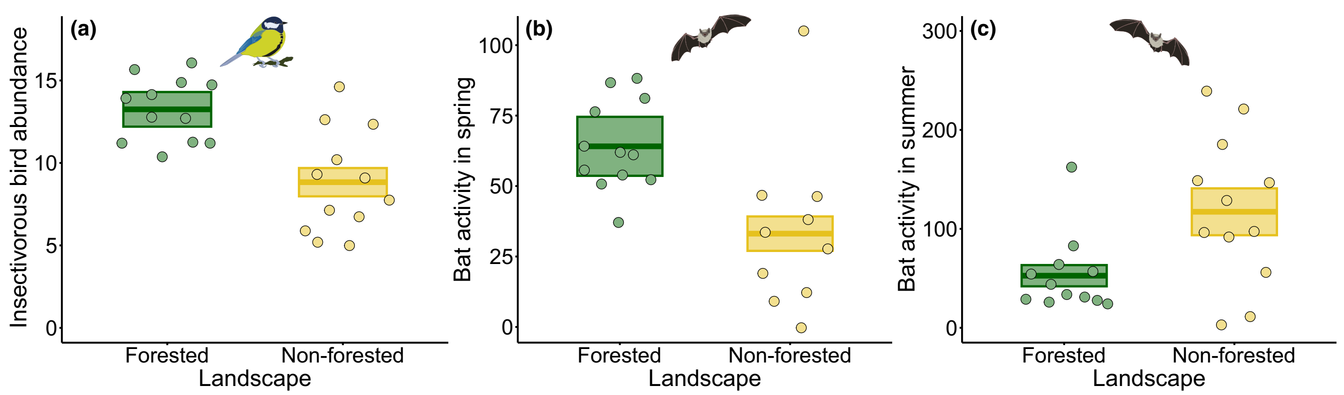

FIGURE 2 Significant effects ($p < 0.05$) of landscape (forested vs. non-forested) on (a) insectivorous bird abundance and (b) bat activities in spring and (c) in summer. On the plots, bold lines indicate model estimates and thin horizontal lines indicate standard errors.

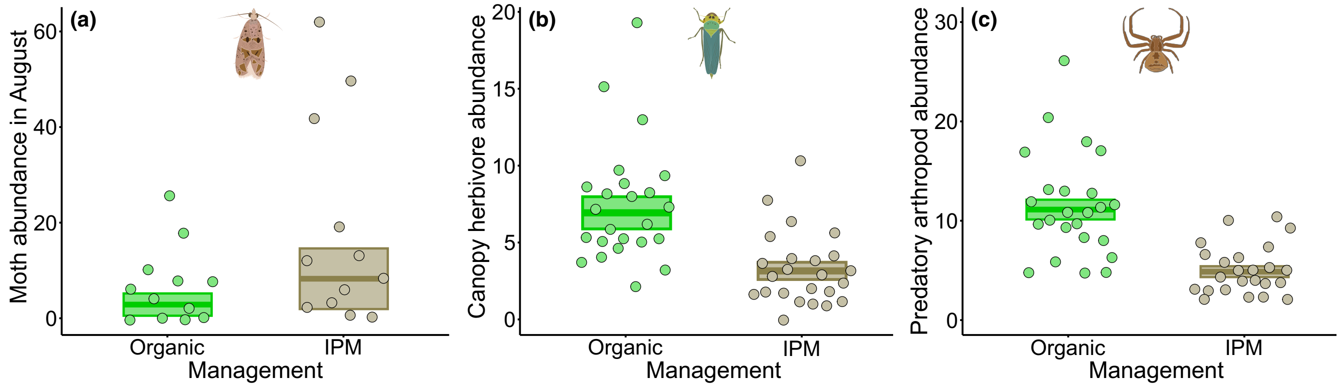

FIGURE 3 Significant effects ($p<0.05$) of management (organic vs. IPM [integrated pest management]) on (a) moth abundance in August and (b) canopy-dwelling herbivorous and (c) predatory arthropod abundances. On the plots, bold lines indicate model estimates and thin horizontal lines indicate standard errors.

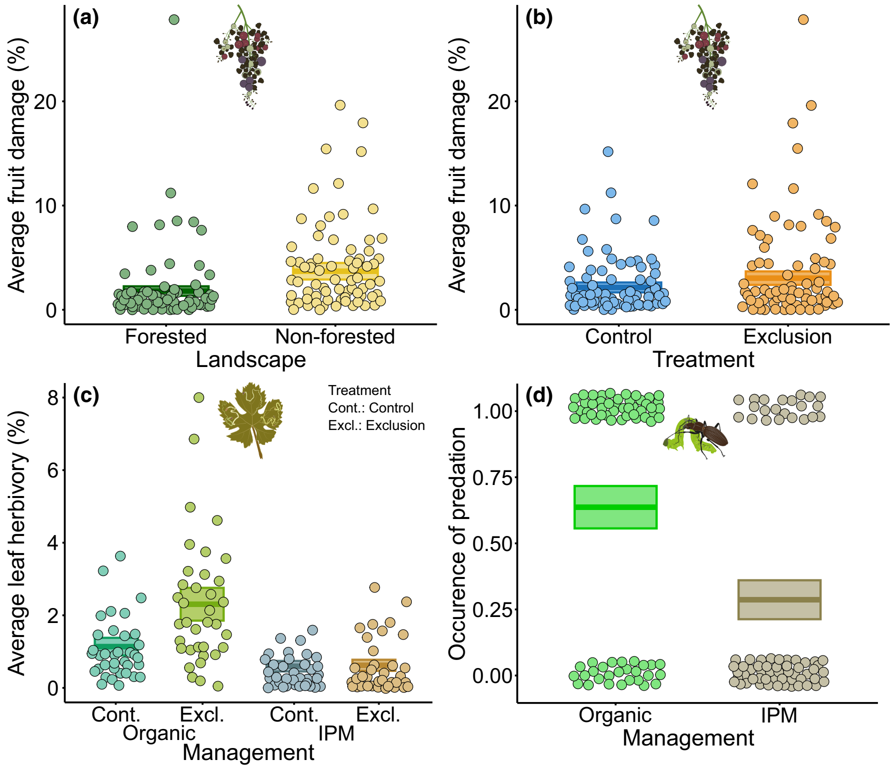

FIGURE 4 Significant effects ($p<0.05$) of (a) landscape (forested vs. non-forested) and (b) treatment (control vs. exclusion) on average fruit damage, (c) significant interacting effect of management (organic vs. IPM [integrated pest management]) and treatment on average leaf herbivory, and (d) significant effect of management on the occurrence of predation on grape plants. Bold lines indicate model estimates and thin horizontal lines indicate standard errors. Data points were jittered for better visibility.

was significantly higher on excluded than control grapes in organic vineyards (1.3% difference, $\chi^2=8.212$, $p=0.004$; Figure 4c). Moreover, organic management significantly and positively affected the occurrence of arthropod-mediated predation on grapes (+104.5%, $\chi^2=9.221$, $p=0.002$; Figure 4d; Table S4).

Regarding functional relationships, moth abundance significantly decreased with increasing bat activity in spring (36.7% lower abundance with an increase of activity from 0 to 100; $\chi^2=3.983$, $p=0.046$; Figure 5a). In addition, average fruit damage significantly increased with increasing overall moth abundance (66.7% higher damage with an increase of abundance from 0 to 100; $\chi^2=6.112$, $p=0.013$; Figure 5b). For further non-significant effects retained after model selection, see Table S4.

4 | DISCUSSION

In our experimental exclosure study, we investigated the role of birds and bats in shaping arthropod abundances and related ecosystem functions in vineyards having contrasting local managements (organic vs. IPM) and landscape heterogeneity (forested vs. non-forested). Besides the scarcity of exclosure experiments for European permanent agrosystems, our study is the first to investigate the biocontrol potential of these vertebrate predators in vineyards by simultaneously accounting for contrasting management and landscape effects. We found that vineyard management only affected canopy-dwelling arthropods, reaching higher abundances and contributing to greater leaf herbivory and predation pressure

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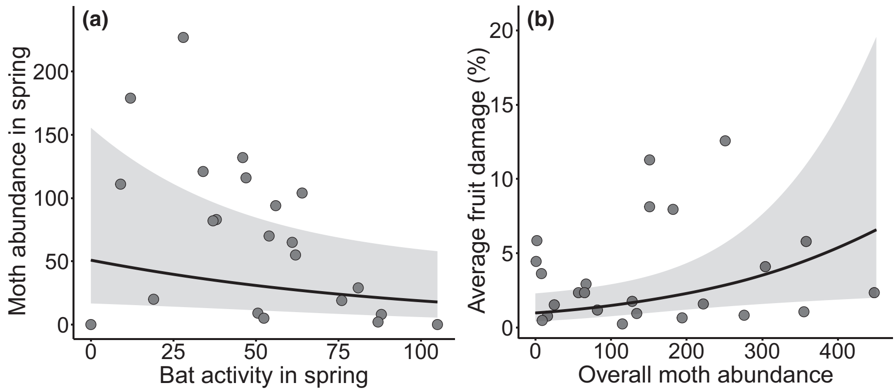

FIGURE 5 Significant effects ($p < 0.05$) of (a) bat activity on moth abundance in spring and (b) overall moth abundance on average fruit damage. Grey bands indicate confidence intervals.

in organic than in IPM vineyards. At the same time, forested landscapes positively impacted insectivorous birds and bats in the breeding period. We also demonstrated that these vertebrate predators act as pest control agents and can potentially reduce herbivory and increase economic benefits.

4.1 | Hypothesis 1: Positive effect of forested landscapes on birds and bats

We found significant effects of forested landscapes on bird abundance and bat activity; however, the latter effect was influenced by the season. In line with previous findings, insectivorous birds benefit from the proximity and availability of forests (Barbaro et al., 2021; Endenburg et al., 2019; Lourenço et al., 2021). These semi-natural habitats provide protected nesting sites, foraging structures, and a considerable amount of food sources (Rösch et al., 2024). Deciduous forests in our study region are dominated by the native sessile oak (*Quercus petraea*), promoting abundant and diverse arthropod communities as food sources for leaf-gleaning insectivorous birds (Mrazova et al., 2023; Valencia-Cuevas & Tovar-Sánchez, 2015).

Forested landscapes can significantly enhance bat foraging activity (Costa et al., 2020; Frey-Ehrenbold et al., 2013). These habitats are particularly important in spring, as they offer prey diversity and roosting microhabitats for many European species (Charbonnier et al., 2016; Dietz & Kiefer, 2016; Veilleux et al., 2003). The preference for less forested sites in summer may arise because bats are no longer confined to wooded areas; by this time, bat juveniles have left the maternity sites (indicated by increased overall activity), enabling them to forage over longer periods and greater distances (Herrera et al., 2024). Although not explored in our study, the relatively high share of open agricultural areas within non-forested landscapes could also provide food-rich hunting grounds for some open-space and edge-space foraging species in this season (Heim et al., 2016). Contrary to our hypothesis, management did not directly affect birds or bats, having similar densities and activities in organic and IPM vineyards. The observed pattern can be attributed to the fact that birds and bats have the highest dispersal ability among the studied taxonomic groups; thus, landscape characteristics might be more decisive in shaping their densities than local factors alone (Assandri et al., 2016; Herrera et al., 2021; Tscharntke et al., 2021).

4.2 | Hypothesis 2: Bats as regulators of moth populations

We found that increasing bat activity negatively affected *L. botrana* abundance in the spring but did not impact canopy-dwelling arthropod densities. Bats are voracious and opportunistic predators, exhibiting numerical responses to increased prey density, including lepidopterans (Ancillotto et al., 2022; Blažek et al., 2021; Wickramasinghe et al., 2004). More specifically, it has been shown that *L. botrana* constitutes a major part of the bats' diet and considerably influences their hunting activity in European wine regions (Baroja et al., 2021; Charbonnier et al., 2021). Indeed, *L. botrana* was the most abundant among the studied arthropods and had the highest density in spring (1791 of 3601 captured individuals); thus, it could be a primary food source for bats in vineyards during this period. In contrast, canopy-dwelling arthropods had relatively low densities, and therefore, they did not represent sufficiently concentrated prey resources for bats. Instead, these groups were affected by the management having higher numbers in organic vineyards due to the release from insecticide (direct effects) and herbicide (indirect effects through reduced herbaceous plant diversity and structural complexity) applications (Tscharntke et al., 2016; Wickramasinghe et al., 2004; Zielonka et al., 2024).

Based on the spatial pattern of bat activity and its negative association with moth abundance in spring, higher *L. botrana* numbers in vineyards far from forests can be expected. One possible explanation for the lack of this observation is that dense and shaded habitats like forests can mitigate hot and dry periods, which are crucial for the development of *L. botrana*, especially in spring (Benelli et al., 2023). This, together with the higher bird and bat activity associated with forests and possibly greater pesticide exposure of simplified agricultural landscapes (Paredes et al., 2021), might result in similar moth density patterns between vineyards with distinct landscape characteristics.

4.3 | Hypothesis 3: Ecosystem services provided by natural enemies

We observed higher leaf and fruit damage in excluded grapes, indicating the potential role of birds and bats in reducing herbivory and increasing crop yield. Accordingly, we also found reduced fruit damage in vineyards situated within forested landscapes, which were preferred by these vertebrate predators in the breeding season. Our results are in line with previous findings showing that bats provide vital ecosystem services, including reduced plant damage and increased economic benefit to farmers (Ancillotto et al., 2024; Rodríguez-San Pedro et al., 2020; Tuneu-Corral et al., 2023). Additionally, bats play a key role in regulating fruit-damaging pests not only in forests but also in surrounding agricultural areas (Ancillotto et al., 2022). In addition, a global meta-analysis showed that birds are important regulators of pest populations, greatly reducing the damage they cause in woody plantations, including vineyards (Monteagudo et al., 2023). At the same time, unlike bats, we were unable to detect a negative relationship between the abundance of birds and the fruit-damaging *L. botrana*. This suggests, on the one hand, that birds were more likely to use the surrounding deciduous forests and their edges as foraging habitats, potentially preventing the spillover of grape pest populations into the vineyards (Boesing et al., 2017; Pithon et al., 2016; Tscharntke et al., 2016). On the other hand, more frequent arthropod sampling (especially in spring) and bird observations (after the breeding season), including assessments of plantation edges, are needed to establish meaningful relationships between bird activity and pest density.

We did not find evidence that birds and bats contribute to lower predation pressure by arthropod natural enemies due to their potentially decreased numbers. Consistent with the density pattern of predatory arthropods, arthropod-mediated predation pressure was more pronounced in organic than in IPM vineyards, and it was unaffected by the exclusion. This may explain the relatively low abundance of *L. botrana* individuals in organic vineyards in August, as spiders, the most abundant canopy dwellers in our study, are considered key predatory arthropods for controlling grape moths (reviewed by Thiéry et al., 2018).

4.4 | Applied perspectives

Our study highlighted that ensuring proximity (30 m on average) and appropriate proportion (25%–40% depending on the spatial scale) of deciduous forest patches around vineyards promotes birds and bats and associated pest regulation and yield increase. These patches are important habitats in the breeding period, especially if they contain a high share of native tree species (e.g. *Quercus petraea* in our study region) having abundant and diverse arthropod communities, hence ensuring valuable foraging resources (Boesing et al., 2017; Charbonnier et al., 2016). The conservation value of these habitats can be further increased by less intensive management practices with the provision of heterogeneous vegetation and large trees to provide suitable nesting and roosting microhabitats (Bereczki et al., 2014; Langridge et al., 2019). Considering the landscape characteristics of the studied vineyards, the importance of woody networks should also be highlighted. Such connectivity through patchy and linear elements (i.e. tree groups, shrublands and hedgerows) can provide optimal foraging habitats and stepping stones for vertebrate predators even in less forested, simplified landscapes (Brambilla & Gatti, 2022; Frey-Ehrenbold et al., 2013; Krings et al., 2022).

Based on our results, bird- and bat-mediated biological pest control can be enhanced by facilitating the colonization of beneficial arthropods in vineyards. This underscores the need to increase the number of organic vineyards. Managing these areas without the use of herbicides and synthetic insecticides, and maintaining adequate herbaceous vegetation height (about 30 cm on average) can support foliage-hunting arthropods, especially spiders, potentially suppressing grape pest populations. Finally, empirical studies showed that other local interventions, such as the provision of structural complexity with native, scattered trees (Herrera et al., 2024; Muñoz-Sáez et al., 2021) and nest boxes and artificial roosts (García et al., 2021; Tuneu-Corral et al., 2023) can help the establishment of bird and bat populations and provide more optimal predation pressure in the plantations.

AUTHOR CONTRIBUTIONS

Péter Batáry, András Báldi and Dávid Korányi conceived the ideas. Dávid Korányi designed the methodology with support from Péter Batáry, Máté Varga and Mattia Brambilla. Dávid Korányi and Sándor Zsebők analysed the data. Dávid Korányi collected the data and led the writing of the manuscript. All authors critically contributed to the drafts and gave their final approval.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest. Péter Batáry is an Associate Editor of the Journal of Applied Ecology but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Digital Repository https://doi.org/10.5281/zenodo.15582643 (Korányi et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Study vineyards situated north of Lake Balaton in Hungary.

Figure S2. Photos of some exclosure plots, including openable cages and six grape plants per plot.

Table S1. Mean ± SE (min–max) values of the local-level variables for the vineyards with organic versus integrated pest management (IPM).

Table S2. Mean ± SE (min–max) values of landscape-level variables for the vineyards situated in forested versus non-forested landscapes.

Table S3. List of the full linear mixed-effect models with fixed and random terms and Moran's *I* tests for the model groups: (1) bird abundances and bat activities depending on the landscape (forested vs. non-forested), management (organic vs. IPM [integrated pest management]), and their interaction; (2) arthropod abundances depending on the landscape, management, treatment (control vs. exclusion; except moths) and their two-way interactions; (3) fruit damage, leaf herbivory, and predation occurrence depending on the landscape, management, treatment and their two-way interactions; and (4) arthropod abundances depending on bird abundances and bat activates, and fruit damage depending on moth abundance.

Table S4. Results of linear mixed-effect model averaging (ΔAICc < 2) and Anova tests (χ^2, *p*) for the model groups: (1) bird abundances and bat activities depending on the landscape (forested vs. non-forested), management (organic vs. IPM [integrated pest management]); (2) arthropod abundances depending on the forest proximity, management, and treatment (control vs. exclusion); (3) fruit damage, leaf herivory, and predation occurrence depending on the forest proximity, management, treatment and their two-way interactions; and (4) arthropod abundances depending on bird abundances and bat activates, and fruit damage depending on moth abundance.

Table S5. List of bird species and their abundances observed during the survey.

Table S6. List of bat taxa and their activities (defined as the number of 5 s intervals containing bat calls) detected during the survey.
Table S7. List of canopy-dwelling herbivorous insect taxa and their abundances collected during the survey.
Table S8. List of canopy-dwelling predatory arthropod taxa and their abundances collected during the survey.
Appendix S1. Supplementary Methods.

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