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Semi-natural habitats are key to breeding bird diversity in intensified vineyard landscapes across Europe

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ABSTRACT

In climatically suitable regions across Europe, vineyards can be the dominant perennial crop type. While many wine-growing landscapes are intensively managed, they may still be an attractive habitat for a wide range of bird species. In this study we investigated how breeding birds in three wine-growing regions in Europe (Germany: Palatinate, France: Bordeaux, Austria: Leithaberg) are influenced by the composition of the landscape, focussing on woody semi-natural vegetation.

We recorded bird vocalizations with autonomous sound recorders in 93 landscapes across Europe. Bird species were identified according to their songs and calls. The landscape in a 200-m buffer around the recording points was mapped. In total, we recorded 72 bird species, including species typical for vineyard landscapes such as cirl bunting (*Emberiza cirlus*), hoopoe (*Upupa epops*) and turtle dove (*Streptopelia turtur*). For all three countries we found that an increase in overall woody vegetation in the landscape led to an increase in species richness and altered community composition. Most species were recorded in landscapes with abundant hedges, small woods and tree rows rather than in vineyard-dominated landscapes but e.g. woodlark (*Lullula arborea*) and linnet (*Linaria cannabina*) showed an opposite preference.

We conclude that in intensively used wine-growing landscapes the ongoing decline in farmland birds and the ecosystem services they provide can be reversed by the reintroduction of semi-natural woody vegetation between vineyards. These in frequently many cases linear structural elements can be established included in the landscape with only small losses in production area.

Introduction

Vineyards are a dominant and highly profitable perennial crop in many regions across Europe. Traditionally, extensively used vineyard landscapes are characterised by a diverse mix of vineyards and semi-natural habitat types like hedges, small woods, grasslands and fallows (Kizos, Plieninger, Schaich, & Petit, 2012) and host a wide variety of species including birds. While the abandonment of vineyards and the subsequent establishment of woody vegetation has had positive effects on bird diversity in some regions (Bonnier, Plieninger, Bhagwat, & Kamp, 2024; Verhulst, Báldi, & Kleijn, 2004), other, more profitable vineyard landscapes continue to be intensified and cleared. Vineyards are thus subject to frequent management interventions including ground vegetation removal through tillage or herbicide use, mulching (Winter et al., 2018) and an intensive use of pesticides compared to other crops (Etienne et al., 2022; European Commission, 2007; Pertot et al., 2017) to increase grape quality and yield. In addition, in many cases, vineyard landscapes have been simplified through land consolidation schemes or due to the use of larger machinery that often led to the removal of semi-natural habitats aiming to increase the production area of this

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highly profitable crop, thus giving vineyard landscapes a monocultural character (Cossart, Fressard, & Chaize, 2020). This development has been exacerbated since, as a permanent crop type, viticulture is excluded from the European Common Agricultural Policy's requirements of designating ecological focus areas (BMEL, 2015; Pe'er et al., 2014). Agricultural intensification in general (Donald, Green, & Heath, 2001) and the removal of structural vegetation elements like hedges in particular, have been identified as a drivers of bird declines (Denac & Kmecl, 2021; Donald et al., 2001; Matson, Parton, Power, & Swift, 1997). Many once common farmland bird species such as turtle dove, yellowhammer or linnet are now increasingly threatened (Grüneberg et al., 2015; Kamp et al., 2021; Schifferli, 2000; Voříšek et al., 2010) showing a steep decline in their population trends across their distribution ranges (https://pecbms.info). However, the patterns of population changes can greatly differ between countries (Tryjanowski et al., 2011; Wretenberg, Lindström, Svensson, Thierfelder, & Pärt, 2006).

While the area of semi-natural habitats within vineyard landscapes is often small, they can strongly contribute to the landscape-wide biodiversity (Poschlod & Braun-Reichert, 2017). For most bird species that occur in vineyard landscapes, shrubs and trees are crucial for nesting, foraging and shelter (Dietzen et al., 2018) and only few species, such as the woodlark, breed directly in vineyards (Bosco, Arlettaz, & Jacot, 2019; Buehler, Bosco, Arlettaz, & Jacot, 2017; Rösch, Aloisio, & Entling, 2021).

In this study we investigate how the diversity and community composition of breeding birds are influenced by the composition of wine-growing landscapes, focussing on woody semi-natural habitats. We selected three study regions in Europe, located in France (Bordeaux), Germany (Palatinate) and Austria (Leithaberg), which are among the respective country's most prestigious wine-growing areas. In all three regions, vineyards are the dominant agricultural land use. Hedges, small woods and other semi-natural habitat structures are widespread albeit unevenly distributed. Therefore, on a relatively small scale, highly

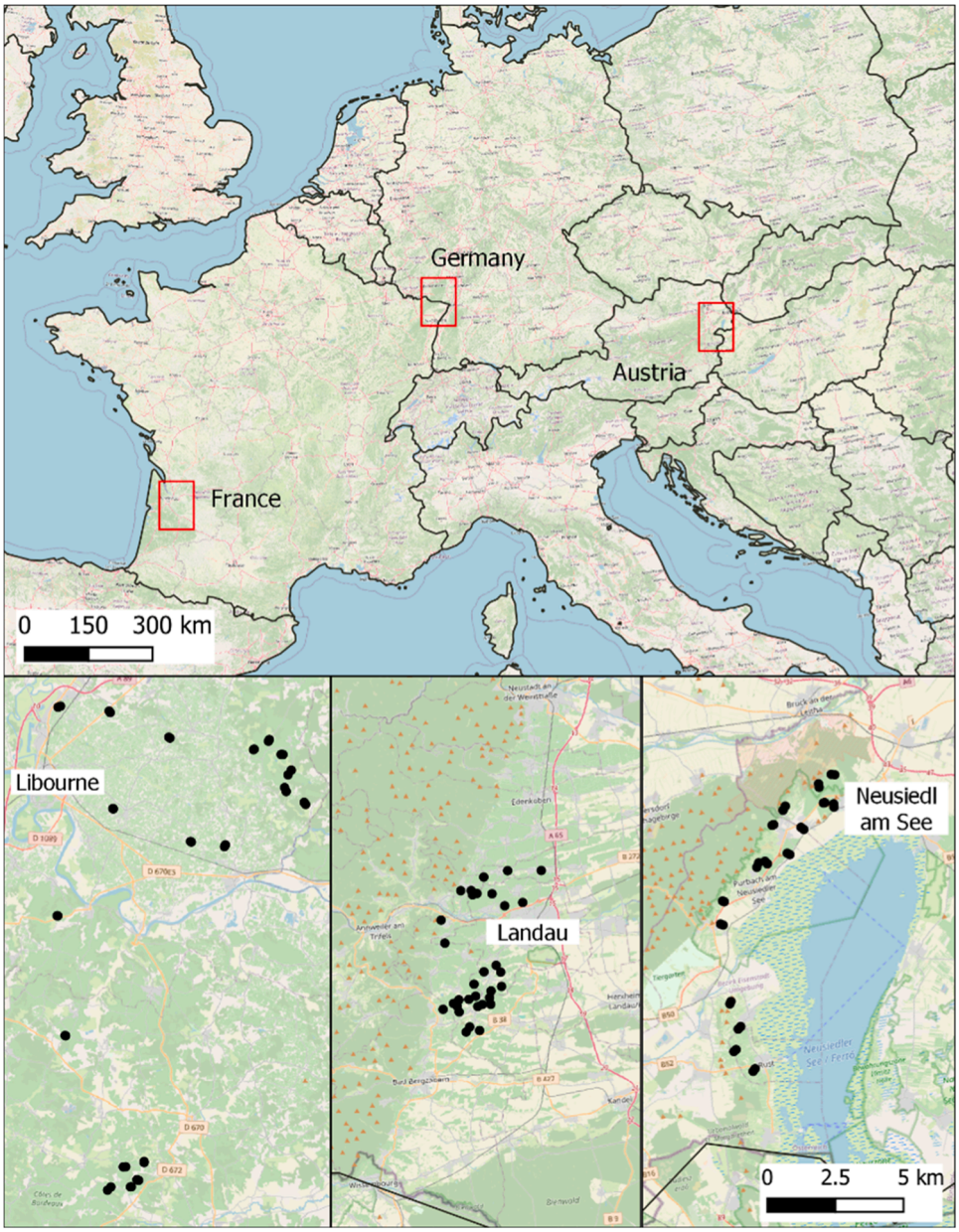

Fig. 1. Map showing the location of the three study areas in France (Bordeaux, Libourne), Germany (Palatinate, Landau) and Austria (Leithaberg, Neusiedl am See). Map data obtained from OpenStreetMap.

simplified landscapes can be found next to more diversified ones.

Specifically, we hypothesise that (1) an increase in woody habitat cover in a landscape leads to an increase in the number of breeding bird species, that (2) the composition of the landscape, i.e. whether it is dominated by vineyards or richer in semi-natural habitat elements, influences the community composition of breeding birds.

Materials and methods

Study areas

The study was conducted in vineyards in three countries: France, Austria and Germany (Fig. 1). In France, the vineyards were located in the Bordeaux region in the areas of Libourne and Entre-deux-Mers (44°54′50″N, 0°14′40″E, 20 m a.s.l.) with a mean annual rainfall of 788 mm and an average temperature of 13.7 °C. In Germany, vineyards were located in the Palatinate at the western margin of the Upper Rhine plain close to Landau in der Pfalz (49°11′54″N, 8°06′45″E, 142 m a.s.l., mean annual rainfall 675 mm, average temperature 10.7 °C) and in Austria in the Burgenland in the Leithaberg region at the western shore of Lake Neusiedl (47°56′34″N, 16°44′09″E, 140 m a.s.l., mean annual rainfall 636 mm, average temperature 11.3 °C, https://de.climate-data.org). In all three areas, vineyards were the locally dominant land use type. The topography of the landscapes was between flat and slightly hilly. Steep slopes were uncommon.

In 2021, in Bordeaux and Leithaberg, around 17% and 22%, respectively, of the vineyard area was under organic management. In the Palatinate region, around 6% of the vineyards were organic. The dominant pesticide group are fungicides, while insecticides and herbicides are far less commonly used. The ground vegetation of the vineyards is mostly managed in an alternating manner, where every second inter-row is tilled during spring while the other inter-row is used for driving. Often, the bare inter-rows are sown with annual ground cover mixtures.

Study design

In all countries, we selected vineyard landscapes of 200 m radius along a gradient in semi-natural habitat cover (both woody and open semi-natural habitat types). In France we selected 29 landscapes and in Germany and Austria 32 landscapes each. Due to the requirements of other parts of the Secbivit project (www.secbivit.boku.ac.at/), in France and Austria, the landscapes were in a paired setup with distances between landscape centres of at least 100 m, in most cases >200 m. The land cover types were mapped in the field and with the help of aerial photographs. Cover types were classified in the following categories (given from highest to lowest cover): vineyards, built-up areas (villages and isolated buildings), arable land with annual crops, woody semi-natural habitat types (forest, woodland patches, hedges, tree rows, single trees and orchards) and open semi-natural habitat types (meadows, pastures, fallows and ruderal areas). Abandoned vineyards were uncommon in all three study regions and were thus not accounted for as an additional land use type. Hedges, woodland patches, tree lines and single trees were widespread throughout the landscapes in all three countries, albeit not evenly distributed, i.e. there were landscapes with a high proportion in semi-natural habitat as well as landscapes that were mostly dominated by vineyards. Therefore, there was a clear negative correlation between vineyard cover and the cover of semi-natural habitat types. In addition, there were country-specific differences, e.g. open semi-natural habitat was commonly found in the landscapes in France and Austria while this habitat type was scarce in Germany (Table 1). Similarly, vineyards were the dominant crop type in France and Germany with hardly any other crops grown in the landscapes we studied. On the contrary, in Austria, arable crops were more common, including cereals, soy beans and sunflowers. Average field sizes varied greatly between regions, with the smallest vineyard units in Austria which resulted in the most diverse landscape mosaic there.

Table 1
Effects of the cover of woody semi-natural habitat (% woody SNH) on bird species richness (Generalized Linear Models).

		Estimate	SE	z	*P*
France	Intercept	2.30	0.09	25.62	**<0.001**
	% woody SNH	0.55	0.10	5.60	**<0.001**
Germany	Intercept	2.51	0.06	39.72	**<0.001**
	% woody SNH	0.02	0.00	3.94	**<0.001**
Austria	Intercept	2.70	0.13	21.05	**<0.001**
	% woody SNH	0.13	0.05	2.63	**0.008**

SE=standard error. P-values <0.05 are shown in bold.

Bird recording and analysis

Birds were mapped with autonomous recording devices (AudioMoth, Open Acoustic Devices, Version 1.1.0) that were set up at a height of 150 cm in the centre of each landscape. Recording was done on days without precipitation and as little wind as possible since the weather strongly influences both the birds' singing activity (Bibby, Burgess, Hill, & Mustoe, 2000) and the recording quality. In order to protect the AudioMoths from humidity, they were covered in a single layer of cling film. In Germany and Austria, recordings were done in 2021 for one day each in April, May, June and July, in France in May, June and July 2020. From each recording date two times 10 minutes were analysed (Bonthoux & Balent, 2012), one at sunrise and the next one an hour after sunrise (e.g. sunrise at 6.21 am, analysis from 6.21–6.31 and from 7.21–7.31) which coincides with the highest singing activity of birds (Bibby et al., 2000).

While surveys using passive acoustic monitoring often analyse longer recording durations (Sugai, Desjonquères, Silva, & Llusia, 2020), the total of 60–80 min per landscape that we analysed should provide a suitable sample to compare bird diversity between temperate agricultural landscapes (Bonthoux & Balent, 2012). Since in Germany we recorded 5–23 bird species per landscape in this study, compared to 0–13 species found breeding along 150 m transects in the same landscapes (Rösch et al., 2023), we would expect that analysing longer recording times would add mostly occasional visitors of the landscapes rather than species that are breeding there. Clearly, our data cover only species that vocalize after dawn, excluding nocturnal species such as the majority of owls. When interpreting our data, it should be kept in mind that species with louder vocalizations have longer detection ranges and are thus overrepresented in our results relative to species with less loud vocalizations (Darras, Furnas, Fitriawan, Mulyani, & Tscharntke, 2018). We did not apply sound level thresholds (Edo, Entling, & Rösch, 2024; Hedley, Wilson, Yip, Li, & Bayne, 2020), since our aim was to characterize landscape level assemblages, not plot level bird assemblages.

The recordings were uploaded into Audacity (version 3.2.2) and resampled at a sampling rate of 22,050 Hz. The visual inspection of the sonograms aided the acoustic identification of songs and calls on the recordings. All songs and calls were identified and noted for each recording, summing up over sampling times and dates, thus also giving an indication for each species' activity in the given landscape.

Statistical analyses

Correlations between land cover types were tested using the functions *cor* and *cor.test* in R version 4.3.1 (R Core Team, 2023). In all countries, vineyard cover and the cover of woody semi-natural habitat were negatively correlated. In addition, in France and Germany there was a positive correlation between the cover of open and woody semi-natural habitat types (Table 2). Statistical analyses were performed separately for each country.

In order to analyse the response of species richness and number of bird territories to woody semi-natural habitat cover, for Germany we

Table 2
Correlations between the different land cover types (%).

		Woody SNH	Open SNH	Vineyards	Built-up areas
France	Open SNH	**0.42**			
	Vineyards	**-0.77**	**-0.83**		
	Built-up areas	0.20	0.31	**-0.44**	
	Arable land	-0.08	0.10	-0.09	-0.19
Germany	Open SNH	**0.39**			
	Vineyards	**-0.82**	**-0.53**		
	Built-up areas	0.32	0.05	-0.14	
	Arable land	0.34	0.25	**-0.79**	-0.13
Austria	Open SNH	-0.22			
	Vineyards	**-0.49**	-0.14		
	Built-up areas	-0.12	-0.13	-0.22	
	Arable land	0.03	**-0.36**	**-0.66**	0.13

Correlations with a *P*-value <0.05 are shown in bold.

fitted generalised linear models (GLMs) with negative binomial errors (function *glm.nb*, R package MASS (Venables & Ripley, 2002)). Due to the nested design of the site selection in France and Austria, we fitted Negative Binomial GLMMs (function *glmer.nb,* R package lme4 (Bates, Maechler, Bolker, & Walker, 2015)) with "site pair" as a random effect. In France in particular, farm buildings and other built-up areas surrounded by trees and other woody vegetation were common in the landscapes. We thus added these areas to the cover of woody semi-natural habitat types in the analyses of species richness. For France and Germany, woody semi-natural habitat cover was $\log_{10}$-transformed to achieve a better fit of the models. Model fit was assessed using AIC, by comparing models without the $\log_{10}$-transformation as well as null models with the final models we used ($\Delta AIC > 2$). Furthermore, model assumptions were checked with the function *simulateResiduals* from R package Dharma (Hartig, 2022).

In order to investigate how individual bird species and indirectly community composition are related to the cover of woody semi-natural habitat we then fitted Multivariate Generalized Linear Models with binomial errors to the presence-absence transformed data of each country using the function *manyglm* from R package mvabund (Wang, Naumann, Wright, & Warton, 2012). The percentage of woody semi-natural habitat was used as explanatory variable, fitting a separate GLM to each species. The function *anova.manyglm* was used for resampling-based hypothesis testing (999 permutations). In *manyglm*, correlations between species are considered, which is not possible using standard GLM tools.

Finally, for each country, the relationship between bird community composition and the cover of four different habitat types (percentage of vineyards, built-up areas, and open and woody semi-natural habitat as explanatory variables) was assessed using partial redundancy analysis (RDA) with presence-absence transformed data with the function *rda* from R package vegan (Oksanen et al., 2013). Since in Austria, unlike in France and Germany, arable land with annual crops made up a significant proportion of the landscapes, it was added as a variable to the analysis here. Species that occurred in fewer than three landscapes were excluded from the datasets prior to analysis. To test for statistical significance, we used a permutation test with 9999 permutations with the function permutest from R package vegan (Oksanen et al., 2013).

Results

In total we recorded over 3000 vocalisations of 72 bird species (51 species in France, 50 in Germany and 46 in Austria). While there were great differences in species composition, the carrion crow (*Corvus corone*) was the most commonly recorded species in all countries (in 88 out of 91 landscapes). In France, the three most commonly recorded species were green woodpecker (*Picus viridis*, recorded in all 29 landscapes), chaffinch (*Fringilla coelebs*, 28) and blackbird (*Turdus merula*, 28). In Germany, magpie *(Pica pica*, in 28 out of 32 landscapes), linnet (*Linaria cannabina*) and great tit (*Parus major*, both 27) were most commonly found, while in Austria, it was pheasant (*Phasianus colchicus*, all 32 landscapes), woodlark (*Lullula arborea*, 27) and nightingale (*Luscinia megarhynchos*, 26). Across the three countries, 16 species of the European farmland bird index (https://pecbms.info/trends-and-indicators/indicators) were recorded, including starling (*Sturnus vulgaris*, 62 out of 91 landscapes), linnet (*Linaria cannabina,* 42), kestrel (*Falco tinnunculus*, 37), cirl bunting (*Emberiza cirlus*, 34) and serin (*Serinus serinus*, 25). Although according to the IUCN list of threatened species only the turtle dove is listed as vulnerable and all other species as least concern, the populations of 39% of the recorded species are declining across their distribution ranges (https://www.iucnredlist.org/).

In all three countries we found a clear positive correlation between bird species richness and the cover of woody semi-natural habitat (Fig. 2, Table 1). In Germany, a very low (<5%) cover of woody semi-natural habitat in the landscape resulted in only 5 to 10 species being present. An increase in woody semi-natural habitat cover to around 5% led to a steep increase to around 15 species. A further increase in woody semi-natural habitat cover resulted in a saturation in the number of species at an average of 20–25 species. In France, bird species richness also saturated at high cover of woody semi-natural habitat, starting at around 15 species at low covers of semi-natural habitat. In Austria, however, there was an approximately linear increase in species richness from 10–15 species at low levels of woody semi-natural habitat cover (0–5%) to 20–25 species at 40% woody semi-natural habitat cover.

For Austria and Germany, the positive relationship of bird species richness with an increasing percentage of woody semi-natural habitat was also confirmed by the Multivariate Generalized Linear Models, i.e. most species were more likely to occur in landscapes with a high percentage of woody semi-natural habitat and only few, including woodlark, linnet and common quail, showed a negative relationship (Fig. 3, Table 3).

Finally, the community composition of the birds in all three countries was influenced by the surrounding landscape (Fig. 4, Table 4). While in all countries many species were predominantly found within landscapes with a high cover of woody semi-natural habitats as well as built-up areas, there were distinct, country-specific patterns as well. In France and Germany few species were associated with landscapes dominated by vineyards. In Austria, however, both open semi-natural habitats and vineyards had a significant influence on community composition.

Discussion

Woody semi-natural habitats had clear positive effects on breeding bird diversity in wine-growing landscapes across Europe. Most of the species were associated with complex landscapes with a high proportion of woody semi-natural habitat while diversity in vineyard-dominated landscapes was much lower, especially in Germany. The cover of woody semi-natural habitat is thus key to a rich bird diversity in intensively used vineyard landscapes and points to a straightforward way to restore the declining populations of farmland birds: the establishment of hedges, small woods, single trees, extensively used orchards or other agroforestry systems (Batáry, Matthiesen, & Tscharntke, 2010; Edo et al., 2024; Rösch, Hafner, Reiff, & Entling, 2023). There seems to be a threshold of around 5% woody semi-natural habitat in the landscape that leads to a steep increase in bird diversity, emphasising that even if the area of semi-natural habitats is small, their contribution to the landscape-wide biodiversity can be considerable (Poschlod & Braun-Reichert, 2017). Reaching this threshold could be facilitated by including perennial crop types like viticulture into the European Common Agricultural Policy's requirements of designating ecological focus areas (BMEL, 2015; Pe'er et al., 2014).

However, the influence of the surrounding landscape was highly

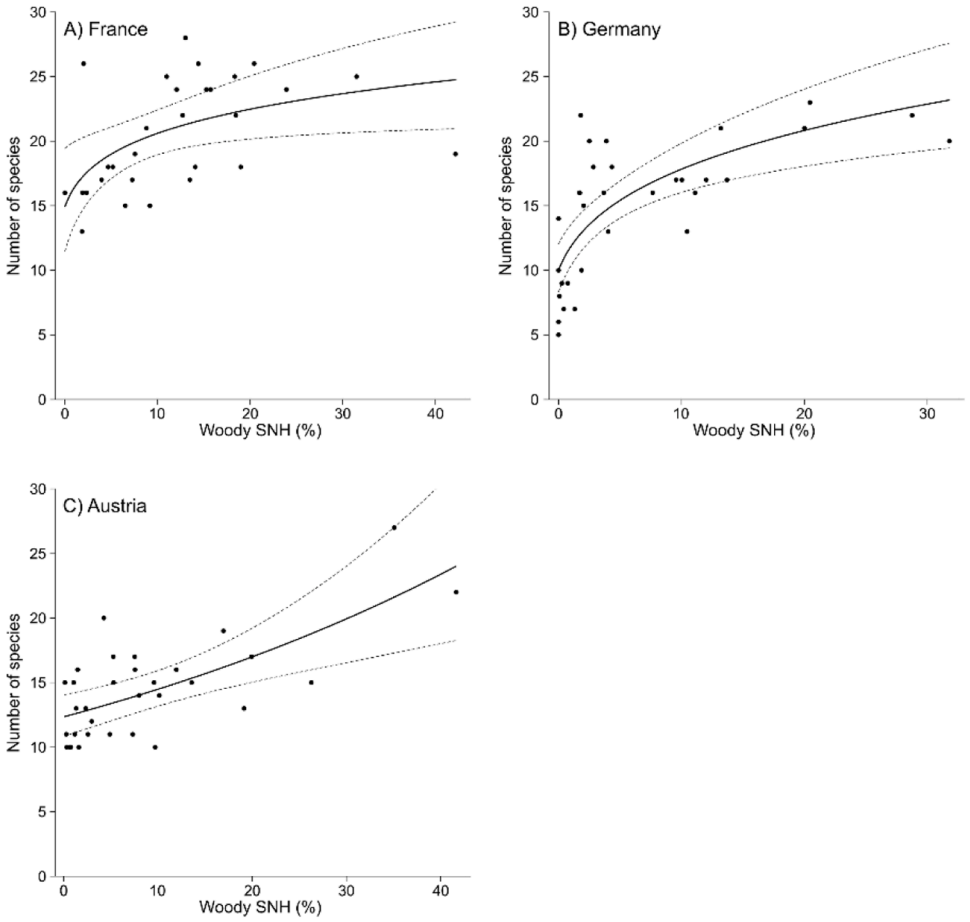

Fig. 2. Relationship between bird species richness and the proportion of woody semi-natural habitat (Woody SNH) in A) France, B) Germany and C) Austria. Regression lines are predictions from General Linear Models (Table 1).

species-specific and to some extent country-specific. While most species showed a positive response to an increasing cover in woody semi-natural habitat, some species were negatively correlated with the cover of woody semi-natural habitat which should carefully be taken into account when planning conservation measures (Barbaro et al., 2021; Besnard & Secondi, 2014; Pithon, Beaujouan, Daniel, Pain, & Vallet, 2016). The woodlark (*Lullula arborea*), a relatively common species in all three regions, is the only species that regularly breeds on the ground directly in vineyards (Bonnier et al., 2024; Buehler et al., 2017; Dietzen et al., 2018; Rösch et al., 2021). In France and Austria, woodlarks were found in most landscapes, irrespective of their composition. However, woodlarks showed a negative correlation with the cover of woody semi-natural habitat in Germany, where the species is critically endangered in the federal state of Rhineland-Palatinate (Simon et al., 2014). An earlier study in the Palatinate region found that woodlarks avoid the vicinity of built-up areas, and are thus commonly found in open vineyard areas (Rösch et al., 2021). Another ground-nesting species that preferred landscapes with a low cover in woody semi-natural habitat, the common quail (*Coturnix coturnix*), has markedly declined over the past decades (BirdLife International, 2004). Despite still occurring over large parts of Europe (Bauer, Bezzel, & Fiedler, 2005), we could only record quails in Austria. The species is unlikely to breed directly in vineyards since it requires high and dense vegetation for nesting (Dietzen et al., 2015; Kosicki, Chylarecki, & Zduniak, 2014) which is scarce in vineyards where the ground cover is often intensively managed through mowing, ploughing or herbicide applications. It has thus likely been calling in adjacent open semi-natural habitat, fallows or crop fields (Kosicki et al., 2014), which, unlike in Germany and France, were relatively common land use types in the Austrian landscapes.

Species with a clear positive correlation with woody semi-natural habitat are shrub-nesting species like chaffinch (*Fringilla coelebs*), typical warblers (*Sylvia* spp.), nightingale (*Luscinia megarhynchos*) and dunnock (*Prunella modularis*). They may attempt to build their nests in the vines' canopy but these attempts have been shown to be largely unsuccessful due to disturbance by agricultural machinery, personnel and management even if new techniques like minimal pruning are introduced, which leads to a denser wine canopy and entails reductions in disturbance frequency (Assandri, Giacomazzo, Brambilla, Griggio, & Pedrini, 2017). Therefore, most species, even ones that nest on or close to the ground like cirl bunting (*Emberiza cirlus*), robin (*Erithacus rubecula*) and yellowhammer (*Emberiza citrinella*), require woody semi-natural habitat elements for breeding successfully in vineyard landscapes (Bauer et al., 2005; Dietzen et al., 2018). As a species with a mostly Mediterranean distribution, the cirl bunting (*Emberiza cirlus*) was recorded in France and Germany but not in Austria (Bauer et al., 2005). While it is rare in Austria and does not occur in the Leithaberg area, the Palatinate region in Germany is at the northern edge of its distribution range. Likely due to climate change, its population size is increasing there (Dietzen et al., 2018). The linnet (*Linaria cannabina*), a species of high conservation value in viticultural landscapes, was found to prefer landscapes dominated by vineyards in Germany where it occurred in the majority of landscapes. In France and Austria, it was far less common and its relationship with the composition of the landscape was not as clear as in Germany. While requiring woody vegetation for nesting, the species commonly feeds on seeds and other plant parts on the ground in vineyards (Bauer et al., 2005).

Apart from providing nesting sites for birds, higher proportions of semi-natural habitats in a landscape have been linked with larger

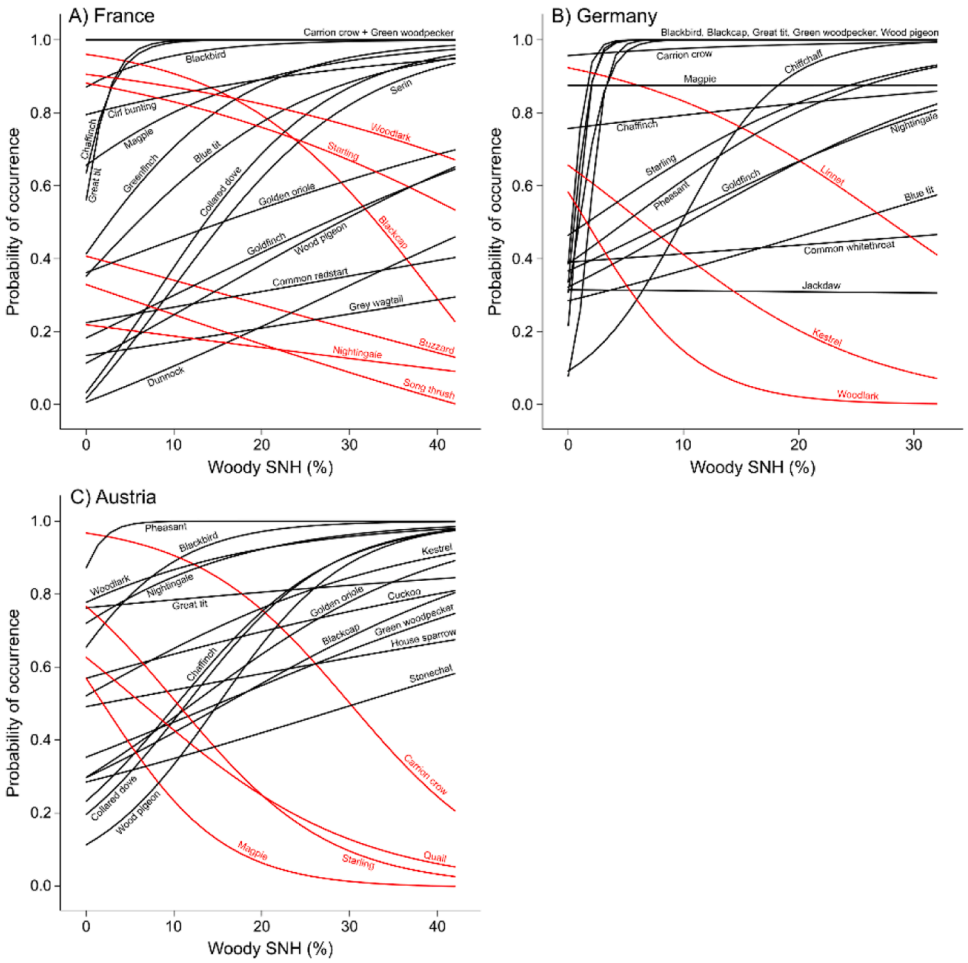

Fig. 3. Relationships of individual bird species with the proportion of woody semi-natural habitat (Woody SNH) in the landscape in A) France, B) Germany and C) Austria. The lines show the predicted probability of the occurrence of the respective species according to Multivariate Generalized Linear Models (Table 3). For better visibility, only species that occurred in more than 10 landscapes in the respective country are shown.

Table 3
Effects of the cover of woody semi-natural habitat (% Woody SNH) on the abundances of the multiple bird species in vineyard landscapes (Multivariate Generalized Linear Models).

		Res. Df	Dev.	*P*
France	Intercept	28		
	% Woody SNH	27	68.83	0.167
Germany	Intercept	31		
	% Woody SNH	30	203.20	**0.001**
Austria	Intercept	31		
	% Woody SNH	30	130.00	**0.002**

Res. Df=residual degrees of freedom. P-values <0.05 are shown in bold.

arthropod diversity and abundance (Kaczmarek, Entling, & Hoffmann, 2023; Kormann et al., 2015; Seibold et al., 2019; Serée, Rouzes, Thiéry, & Rusch, 2020). High arthropod abundances are crucial since during the breeding season, the largest part of the species we recorded require arthropods to raise their chicks (Bauer et al., 2005). While the ground cover vegetation in vineyards may be suitable for foraging species like starling (*S. vulgaris*), rook (*Corvus frugilegus*), carrion crow (*Corvus corone*), chaffinch (*Fringilla coelebs*), buntings (*Emberiza* spp.) and linnet (*Linaria cannabina*), others, including tits (*Parus* spp.) and typical warblers (*Sylvia* spp.), mostly require woody vegetation to forage (Dietzen et al., 2018). Arthropod availability in the ground cover vegetation could be increased by the establishment of diverse swards in the inter-rows since plant species richness and arthropod diversity and abundance have been found to be correlated (Haddad et al., 2009; Siemann, Tilman, Haarstad, & Ritchie, 1998). Another option to improve arthropod availability could be the establishment of diverse, structurally complex margins, fallows or other non-crop areas (Carlos et al., 2019; Gaigher et al., 2024). In addition to arthropod abundance, their accessibility is a key issue, and management that entails patches of low vegetation or open soil is crucial for many ground-foraging bird species (Schaub et al., 2010).

Although targeted at fungi, fungicides can negatively affect arthropods in vineyards (Möth et al., 2023; Pennington et al., 2019) and a reduction in the number of sprayings has been shown to have a positive effect on arthropod abundances (Kaczmarek, Entling, et al., 2023; Kaczmarek, Gillich, Entling, Hoffmann, & Schirmel, 2023; Reiff, Sudarsan, Hoffmann, & Entling, 2023). A solution could be the planting of new fungus-resistant grape varieties which allows for a considerable reduction in the number of fungicide applications that dominate the plant protection regime in vineyards (Reiff et al., 2023). In addition, a lower number of sprayings entails a reduction in disturbances caused by management interventions with agricultural machinery. If adopted on a landscape scale, the use of fungus-resistant varieties could thus be beneficial for both bird species that are nesting in vineyards and those which use them for foraging.

Conclusion

The studied vineyard landscapes in Austria, France and Germany

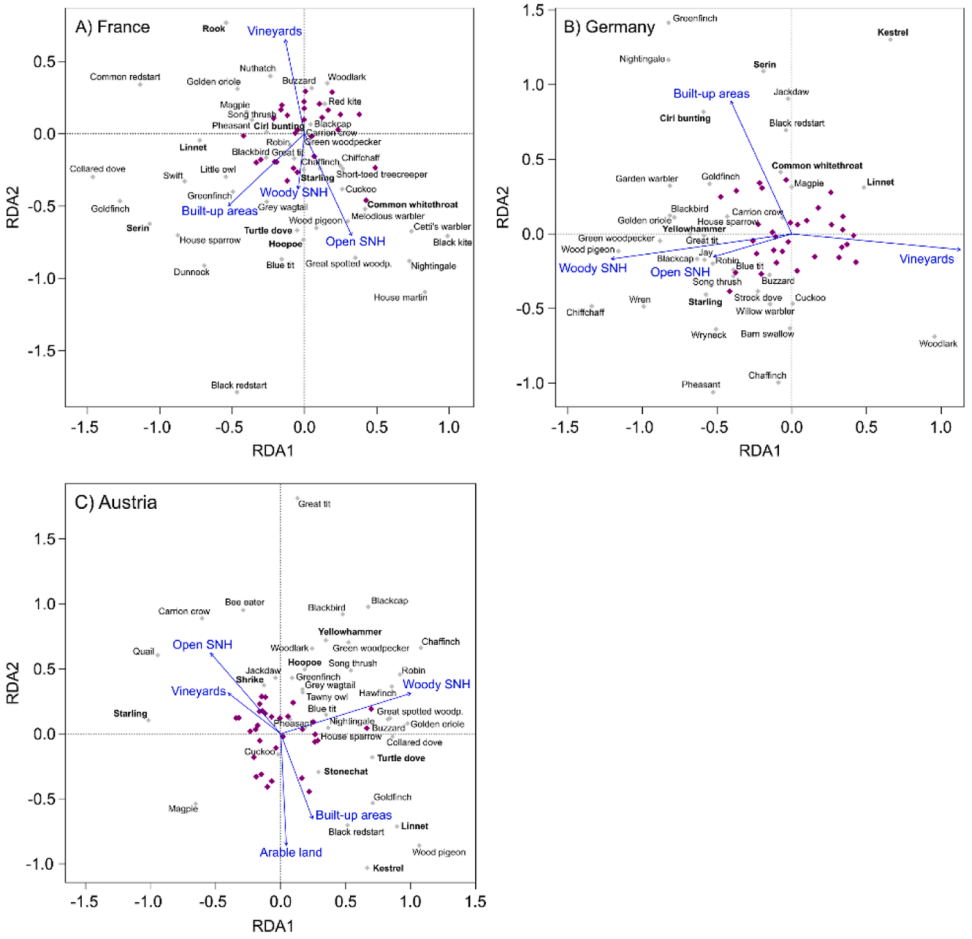

Fig. 4. RDA plots showing differences in bird communities depending on the composition of the landscape around vineyards in A) France, B) Germany and C) Austria. Purple diamonds indicate landscapes while grey diamonds indicate species. Species that are part of the European farmland bird index are shown in bold letters.

supported a wide range of farmland birds, many of which show decreasing population trends in Europe. The large majority of these species, for example serin, wryneck and yellowhammer, is dependent on woody semi-natural habitat elements in the landscape for both nesting and foraging. Only few species, including woodlark and linnet, prefer landscapes dominated by vineyards.

We therefore conclude that in intensive wine-growing landscapes across Europe the ongoing decline in farmland birds could be reversed by the reintroduction of semi-natural woody vegetation between vineyards, ideally supported by off-field agri-environmental schemes. These in frequently many cases linear structural elements like hedges and tree lines can be included in the landscape with only small losses in production area but significant benefits for biodiversity. However, given the contrasting response of some bird species to landscape composition, effective measures require careful planning in the light of local conservation priorities. Additional benefits to breeding birds can be expected by vineyard management that improves the vegetation structure or the availability of arthropod prey for birds.

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CRediT authorship contribution statement

Verena Rösch: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation. **Fernanda Chavez:** Writing – review & editing, Methodology, Investigation. **Lasse Krey:** Methodology, Investigation. **Stefan Möth:** Writing – review & editing, Resources, Methodology, Conceptualization. **Božana Petrović:** Methodology, Investigation. **Sylvie Richart-Cervera:** Writing – review & editing, Methodology, Investigation. **Adrien Rusch:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Mareike Tiedemann:** Methodology, Investigation. **Pauline Tolle:** Writing – review & editing, Methodology, Conceptualization. **Leon Weyandt:** Methodology, Investigation. **Silvia Winter:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Martin H Entling:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Table 4
Mean cover ± SD of the different habitat types as well as results of partial RDA analyses: influence of vineyard cover, built-up areas, arable land with annual crops (only in Austria) as well as woody and open semi-natural habitat (SNH) on the community composition of birds in France, Germany and Austria.

	Habitat type	Mean cover (%)	±	SD	partial RDA % of variation	F	P
France	Vineyards	66.14	±	15.77	4.35	1.31	0.131
	Built-up areas	3.07	±	3.46	6.41	1.93	**0.004**
	Open SNH	20.08	±	8.41	4.14	1.24	0.186
	Woody SNH	9.24	±	8.07	4.98	1.50	**0.043**
	Total				20.23	1.52	**<0.001**
Germany	Vineyards	87.97	±	15.07	4.53	1.61	**0.035**
	Built-up areas	0.27	±	0.61	5.59	1.99	**0.007**
	Open SNH	0.70	±	2.65	3.62	1.29	0.153
	Woody SNH	6.67	±	8.22	5.56	1.98	**0.007**
	Total				24.18	2.15	**<0.001**
Austria	Vineyards	58.72	±	17.63	4.29	1.60	**0.046**
	Built-up areas	1.25	±	4.88	4.49	1.67	**0.023**
	Arable land	16.70	±	14.36	4.37	1.63	**0.041**
	Open SNH	12.82	±	10.13	4.45	1.66	**0.029**
	Woody SNH	7.53	±	9.57	4.49	1.67	**0.026**
	Total				30.21	2.25	**<0.001**

P-values <0.05 are shown in bold.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

All data used for the analyses in this paper are available from the figshare database (accession number 10.6084/m9.figshare.27054997).

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