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Organic management and landscape heterogeneity combine to sustain multifunctional bird communities in European vineyards

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Abstract

1. Conserving functionally diverse bird communities in European farmland is becoming critical, with no exception for regions of wine production. Management intensification combined with the loss of semi-natural habitats in wine-growing landscapes has led to a long-term decline not only in birds of conservation concern but also in once common insectivores and seed eaters. These declines are expected not only to threaten key ecological services provided by vineyard birds, such as pest or weed control, but also their cultural significance.
2. We analysed how organic management and landscape heterogeneity affected taxonomic and functional diversity of 334 bird communities from 12 regions of the three main wine-producing European countries (France, Italy and Spain). We further modelled the responses of community-level metrics measuring mean habitat specialization and bird song attractiveness to humans, as well as cumulative abundances of functional insectivores, seed and grape eaters to account for individual avian functions.
3. We found that organic viticulture enhanced bird functional diversity and individual functions, but that its positive effect partially depended on grass cover management in the inter-rows and landscape heterogeneity. Woodland cover and landscape compositional heterogeneity increased both taxonomic and functional diversity of bird communities, as well as functional insectivory. Landscape

Clélia Sirami and Adrien Rusch contributed equally to this work.

configurational heterogeneity also increased functional diversity and mean song attractiveness of bird communities.

4. Overall, both bird diversity and functions were enhanced by higher landscape heterogeneity, especially in organic vineyards. However, mean habitat specialization decreased with woodland cover and configurational heterogeneity, meaning that open habitat specialists preferred more even landscapes with high vineyard cover.
5. *Synthesis and applications*. Our study highlights the benefits of combining organic management and partial grass cover at the field level and promoting interfaces between vineyards and semi-natural habitats at the landscape level to sustain multifunctional bird communities in wine-producing European countries.

KEYWORDS

bird cultural significance, bird functions, compositional heterogeneity, configurational heterogeneity, functional diversity, grass cover, landscape diversity, song attractiveness

1 | INTRODUCTION

Intensification of agricultural practices during the last decades has caused profound changes in bird communities world-wide (Hendershot et al., 2020). Intensive farming has not only threatened already rare species (Sykes et al., 2020), but also the provision of key functions delivered by bird communities, such as pest control or seed dispersal, while increasing potential disservices (Smith et al., 2020). The interplay between farming practices and landscape structure can mitigate, improve or dampen the synergies between multiple ecosystem functions and services provided by biodiversity in farmland (Martin et al., 2019; Redhead et al., 2020), including those provided by birds (Pejchar et al., 2018; Whelan et al., 2015). Viticulture is of major economic importance in Europe and currently faces important environmental challenges that lead wine growers to shift towards more environmentally friendly management, such as organic farming or use of permanent grass cover (Merot et al., 2019). As vineyards are likely to expand more and more at the expense of semi-natural vegetation with climate warming (Hannah et al., 2013), it is critical to better understand the combined effects of field management and landscape context on bird diversity across a large range of wine production areas.

In Europe, vineyards are managed with various intensification levels, but generally result in heterogeneous mosaics of semi-natural habitats interspersed with large areas of grape dedicated to wine production. However, the combined effects of land use and climate changes, together with the use of agrochemicals and changes in soil management, induced a loss of landscape heterogeneity in European vineyards (Paiola et al., 2020; Paredes et al., 2021). Landscape homogenization is a key driver of biodiversity dynamics in agricultural landscapes (Fahrig et al., 2011), which can dampen ecological services such as natural pest control provided by insectivorous birds (Assandri et al., 2016; Jedlicka et al., 2011; Lourenço et al., 2021). Maintaining landscape heterogeneity is therefore of critical importance for biodiversity conservation as well as for the provision of multiple ecological functions and services (Winqvist et al., 2011).

The conservation of vineyard bird communities has received little attention in Europe, mainly because vineyards are often considered species-poor agroecosystems (Brambilla & Ronchi, 2020). However, vineyards have historically supported, and could still potentially host typical bird communities including threatened specialists such as Lesser Grey Shrike *Lanius minor* or Ortolan Bunting *Emberiza hortulana*, now extirpated from most of these formerly used habitats (Brambilla, Gustin, et al., 2017; Isenmann & Debout, 2000). Other species of conservation concern, such as Great Bustard *Otis tarda*, Little Bustard *Tetrax tetrax* or Stone Curlew *Burhinus oedicnemus*, have also disappeared from most vineyard landscapes following management intensification and may not persist without sufficient scrub/grassland patches in the landscape (Casas et al., 2020). More generally, the long-term decline of insectivorous birds in vineyards is directly related to the loss of semi-natural grasslands and crop intensification (Bowler et al., 2019). Birds provide multiple ecosystem services to viticulture, including biological control of insects and weeds (Whelan et al., 2015), as well as cultural values (Brambilla, Ilahiane, et al., 2017; Cumming & Maciejewski, 2017). As a result, conserving functionally diverse bird assemblages in vineyards is becoming critical, given the social and economic importance of this permanent crop production under Mediterranean-type climates (Muñoz-Sáez et al., 2020; Paiola et al., 2020).

Vineyard bird assemblages are highly dependent on multi-level habitat heterogeneity created by both inter-row management of grass and bare ground cover (Duarte et al., 2014; Guyot et al., 2017) and semi-natural habitat diversity at the landscape level (Assandri et al., 2016; Muñoz-Sáez et al., 2020). Organic farming and extensive grass cover can benefit birds through higher availability of food resources (weeds and arthropods) or nesting sites (Fuller et al., 2005; Winqvist et al., 2011), while higher landscape heterogeneity increases complementation between key resources distributed over the entire landscape matrix (Dunning et al., 1992). Moreover, the interplay between compositional and configurational landscape heterogeneity can modulate the local effects of management practices on bird communities (Martin et al., 2019). The benefits of organic farming or extensive grass cover management should therefore be maximal in more homogeneous landscapes than in more diverse mosaics where resource availability and habitat diversity are already high and the gains of agroecological practices likely low (Tscharntke et al., 2012; Tuck et al., 2014). The effect of organic farming on vineyard bird diversity is still seldom studied although organic vineyards are rapidly expanding in some countries such as France, Italy and Spain (Assandri et al., 2016; Rollan et al., 2019). So far, previous studies did not consistently find direct and positive effects of local organic farming on insectivorous birds or bats. Instead, several studies have reported interacting effects of organic management with grass cover, landscape composition and availability of arthropod prey (Froidevaux et al., 2017; Rodríguez-San Pedro et al., 2019; Winter et al., 2018).

Here, we investigated how organic farming interacts with other management options and landscape heterogeneity, across a large range of wine-producing regions of southern Europe, to shape vineyard bird diversity. We built a multi-regional dataset to test how the different components of bird communities, including taxonomic and functional diversity as well as individual avian functions, display consistent and complementary responses to vineyard management at both local and landscape levels. We specifically predicted that: (a) the effect of organic management would be positive on both taxonomic and functional bird diversity because of wider foraging niche opportunities; (b) the effect of organic management would interact with both inter-row grass cover and landscape heterogeneity; (c) the effect of landscape composition would be predominant for bird taxonomic diversity and community composition, by filtering the regional species pool able to use vineyards at the local scale; and (d) the effect of landscape configuration would be stronger on functional diversity and individual functions because it primarily increases resource complementation for birds between vineyards and the wider landscape.

2 | MATERIALS AND METHODS

2.1 | Study areas

We studied 12 wine-growing regions located in three countries of southern Europe that are the three main producers of wine worldwide: France (nine regions), Italy (two regions) and Spain (one region; Figure 1). The proportion of organic versus conventional management and the extent of landscape heterogeneity covered varied among regions (Appendix S1). In each region, vineyards were selected along a landscape compositional gradient based on the proportion of woodlands and semi-natural grasslands in the surrounding landscape. For each stand, we determined the type of management (organic or conventional) by local inquiries combined with information gathered by dedicated professional structures (e.g. DOQP bureau in Spain). The proportion of organic stands was 31% in the

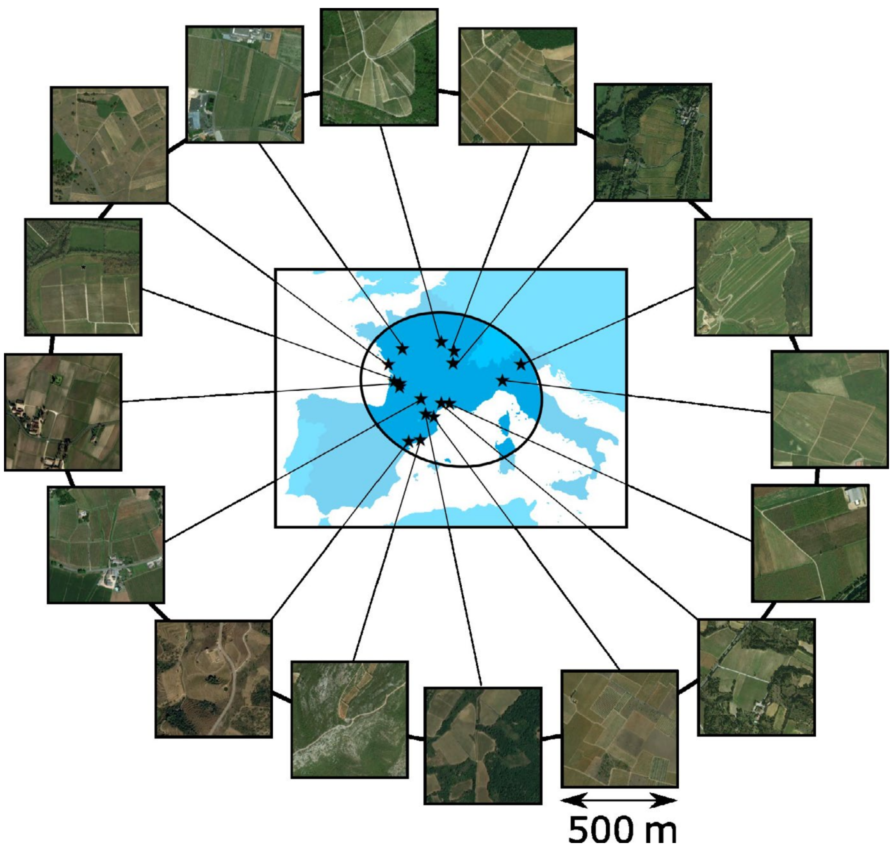

FIGURE 1 Location map of sampled wine production regions. Clockwise from top: Bourgogne (3 subregions), Trentino, Lombardy (Oltrèpo Pavese), Costières de Nîmes, Terrasses du Larzac, Corbières, Limoux, Catalunya (Priorat and Penedès), Gaillac, Bordeaux Saint Emilion, Bordeaux Médoc, Ile de Ré, Saumur

overall dataset (N = 103 vs. N = 231 for conventional stands). We also measured the proportion of grass cover in vine inter-rows, ranging between 100% (homogeneous grass cover) and 0% (bare ground), while a value of 50% indicates partial grass cover due to soil tillage in half of inter-rows. Mean grass cover over all plots was 52% and the distribution of continuous values of grass cover was well balanced between 0% and 100%.

2.2 | Bird sampling

Bird communities were sampled within a single year in each study region, but in different years according to the region, from 2010 to 2018. However, 85% (i.e. 285 among the 334 plots) were sampled either in 2013 or 2015, with no bias towards organic or conventional vineyards in a particular year (Appendix S2). Birds were surveyed using point or transect counts by single trained observers per region. All birds heard and seen were recorded except flyovers, within a distance of 50 to 100 m from the observer on each transect side, depending on the region. Point counts were performed using a standard distance detection of 100 m. To account for differences in the area sampled between circular points and transect counts, we included the sampled area as a random model predictor. We assumed that variation in species detectability was limited among sampled vineyards due to the highly similar and homogeneous structure of vine rows. Bird counts were performed early in the morning (06:00 to 10:00 a.m.) only during days without heavy rain or wind. Bird counts were conducted twice, the first visit between mid-April (early-season breeders) and mid-May and the second visit between late May and mid-June (late-season breeders), except in Italy where a third visit was conducted between these two visits. For each species, the highest count among the two or three visits was further used as a standardized estimate of abundance.

2.3 | Bird community metrics and functions

We analysed the responses of six community-level metrics, including bird taxonomic diversity, functional diversity, conservation concern and cultural significance, as well as three abundance-based avian functions. We calculated the Shannon index of taxonomic diversity to account for both species abundance and richness of bird communities. We further computed three trait-based functional metrics expected to support the largest diversity of species functions, that is, functional divergence, evenness and entropy (Mouillot et al., 2013). We used a species-trait matrix of eight life-history traits, including six categorical traits (foraging method, adult diet, nesting site, migration strategy, mean laying date and mean home range size) and two continuous traits (clutch size and body mass). Functional divergence (FDiv) measures trait abundance distribution and increases with extreme trait values, functional evenness (FEve) increases with the regularity of trait abundance distribution, while Rao's Q functional entropy characterizes species dispersion from the functional space centroid, that is, it indicates a community composed of species functionally different from the mean trait composition (Mouillot et al., 2013).

Following Blackburn et al. (2014), we considered mean bird song attractiveness to humans as a proxy for bird cultural significance, by calculating the number of individual species recordings uploaded in Xeno-canto.org online database (Vellinga & Planqué, 2015), weighted by geographical range size (XCRw). Bird conservation concern was expressed as mean bird habitat specialization, which can be considered as one of the main forms of ecological rarity (Godet et al., 2015; Sykes et al., 2020). We used the Community Generalization Index (CGI), that is, the community-weighted mean value of all Species Generalization Indices (SGIs) within a given community. The SGI is a measure of species ecological rarity quantifying habitat niche width for a given species. It is defined as the coefficient of variation of the species density across 18 habitat classes sampled at the national scale and corresponds to the inverse value of the Species Specialization Index (Godet et al., 2015).

To characterize individual avian functions within bird communities, we computed the cumulative abundance for several functional guilds of species that potentially—but not necessarily always—benefit viticulture (pest control: functional insectivores FI; weed control: seed eaters SE) or may be considered as vine pests (grape eaters GE). To assess potential insect pest control, we calculated the index of Functional Insectivory by cumulating the abundance of species sharing a similar combination of diet, foraging technique and habitat use (Barbaro et al., 2017). A bird species was considered a 'functional insectivore' in vineyards when it was simultaneously: (a) insectivorous during the breeding period; (b) predominantly foliage gleaner or hawker; and (c) using vineyards as breeding and/or foraging habitats (N = 34 species; see Appendix S4). To assess potential weed control and grape damage, we computed similarly the abundance of seed eaters SE (N = 17 species) and grape eaters GE (N = 9 species). Seed-eating birds were determined based on their diet preferences during the breeding season, and grape consumers from a literature survey completed by expert knowledge.

2.4 | Landscape variables

Land covers were mapped with ArcGIS 10.6 (ESRI) for all regions using the following standard nomenclature: woodlands and hedgerows, grasslands, shrublands, crops, vineyards, orchards, roads, urban areas and bare ground. For France, land cover maps were derived from two sources, the BD Topo version 2 of Institut Géographique National 2018 and the Cesbio OSO2018 online database in vector format downloaded from http://osr-cesbio.ups-tlse.fr/~oso (Inglada et al., 2018). For Italy and Spain, land cover maps were obtained from photo-interpretation of aerial photographs at 1:2,000 combined with pre-established land cover maps using the same nomenclature as above; taken from www.geoportale.regione.lombardia.it for Lombardy (Brambilla, et al., 2017); from Assandri et al. (2016) for Trentino; and from a DMAH land cover map of 2005 for Catalonia (Puig-Montserrat et al., 2017). For each vineyard, we computed four landscape variables within 100-m radius buffers, after checking in a multi-scale analysis that larger buffer sizes were not more informative (Appendix S5). We calculated two variables of landscape composition (% of semi-natural open habitats SNOH and % of woodlands) and two variables of landscape heterogeneity, both compositional, using the Shannon diversity index of land cover types (hereafter 'landscape diversity'), and configurational, by calculating the total length of edges between all vineyard patches and all types of semi-natural habitats (Fahrig et al., 2011).

2.5 | Statistical analysis

We performed a set of generalized linear mixed models (GLMMs) to test the relative effects of vineyard management (organic vs. conventional), grass cover and landscape heterogeneity on nine bird community metrics and individual avian functions computed for 334 bird communities: species diversity SDiv, CGI, mean song attractiveness XCRw, functional insectivore abundance FI, seed eater abundance SE, grape eater abundance GE, functional divergence FDiv, functional evenness FEve and functional entropy RaoQ (Figure 2). GLMMs were built in R software v3.6.0 (R Core Team, 2020) using the GLMMTMB package (Brooks, 2020). Three community metrics were count data (sum of species abundance for distinct foraging guilds) and were modelled using Poisson distribution (FI and GE) or quasi-Poisson (SE) distribution to handle over-dispersion. All other metrics (taxonomic and functional diversity, CGI and XCRw) were modelled using the Gaussian distribution after checking for normality and heteroscedasticity of residuals using Shapiro–Wilk tests.

We used the same full model structure for all response variables, including the following fixed effects: the interaction between vineyard management (organic vs. conventional) and inter-row grass cover, the interactions between organic management and landscape compositional (Shannon habitat diversity) and configurational heterogeneity (length of vineyard—semi-natural habitat edges), and two variables of landscape composition (% of semi-natural open habitats and woodlands). The region of wine production ($N = 12$) was considered as a random effect to account for spatial gathering of sampled stands, biogeographical differences and for the combination of year and observer effects. We also included the area sampled as a second, additive random effect to account for differences in sampling protocols among regions. Because we expected a possible effect of sampling protocol on abundance-based metrics (SDiv, FI, GE and SE), but not on integrative community indices (CGI, FDiv, FEve, Rao's Q and XCRw), we also tested the area sampled as an offset in mixed models structure for bird guilds but found no differences in model performances (Brooks, 2020). All continuous variables were standardized (i.e. rescaled to the same unit) to enable comparisons of effect magnitude.

We evaluated multicollinearity among predictors with both the variance inflation factor (VIF) and the Spearman's correlation test;

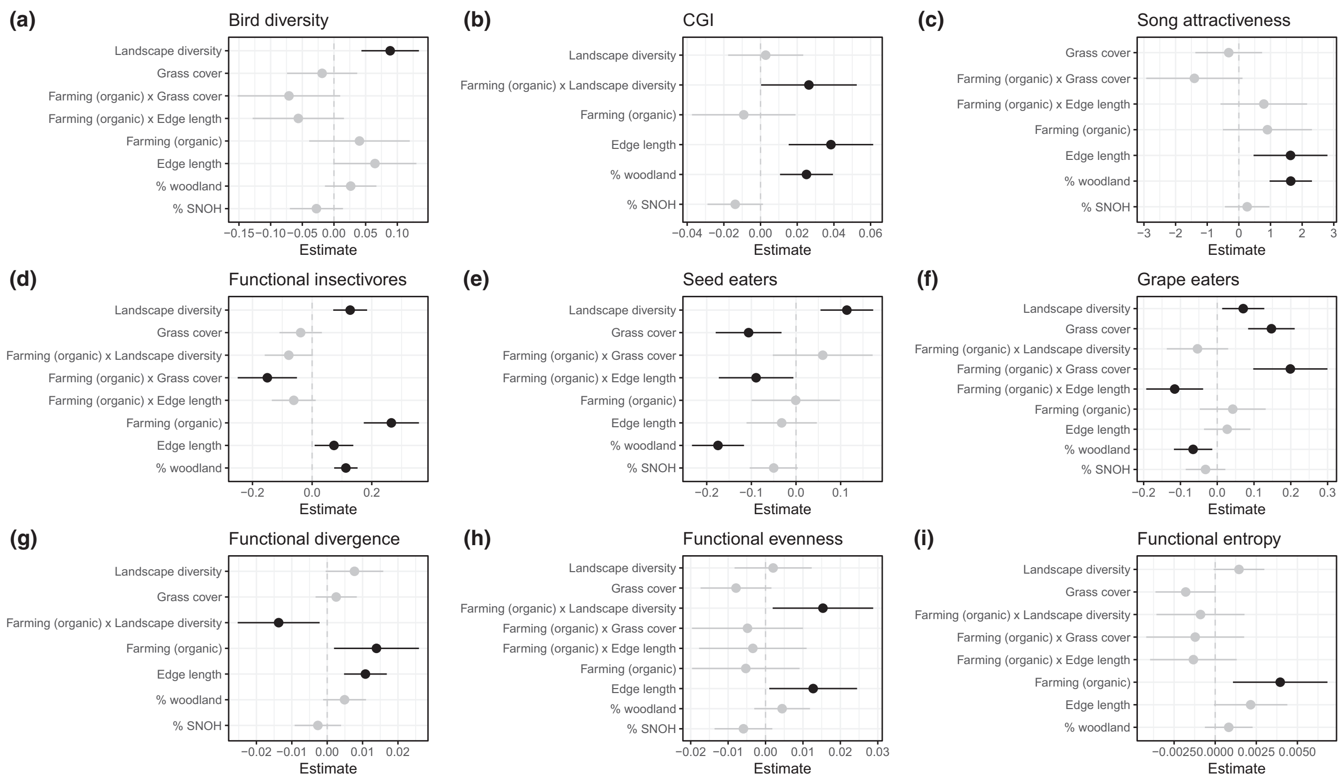

FIGURE 2 Estimates and confidence intervals of conditional averaged models for bird community metrics (a–c), individual functions (d–f) and functional diversity (g–i). Bold intervals indicate predictor significance at $p < 0.05$ (±95% confidence intervals). CGI is the Community Generalization Index, SNOH means Semi-Natural Open Habitats

no strong correlation was found (VIF values < 3; |*r*| < 0.6). Model validation was conducted using the DHARMa package (Hartig, 2020). We performed the Shapiro–Wilk test on LMMs' residuals to ensure that normality assumptions were met. Based on the full models, we generated a set of candidate models containing all possible variable combinations using MuMIn package (Bartoń, 2020). We applied an information theoretic approach to assess model parsimony and models were ranked based on their Akaike information criterion (AIC). To account for model selection uncertainties, we performed a model-averaged procedure of most parsimonious models (i.e. those with ΔAIC < 2), and further report the conditional model average estimates. We checked model residuals for the absence of spatial autocorrelation using bubble plots and variograms and drew prediction biplots based on the best and most parsimonious models.

3 | RESULTS

Bird sampling of 334 vineyards across 12 wine-growing regions from three countries gave a total count of 11,472 individuals belonging to 131 species. Among the taxa of high conservation concern in Europe, we recorded the presence of *Tetrax tetrax*, *Burhinus oedicnemus*, *Galerida theklae*, *Oenanthe hispanica* and *Emberiza hortulana* (Appendix S3). The abundance of functional insectivores and the functional diversity of birds (both divergence and entropy) significantly increased with organic management (Figure 2). For functional insectivores and grape eaters, the positive effect of organic management was contingent upon inter-row grass cover, with reverse patterns (Figure 3). By contrast, the abundance of seed eaters decreased with grass cover (Figure 2).

Woodland cover significantly increased the abundance of functional insectivores, habitat generalists (i.e. it decreased mean bird specialization) and mean song attractiveness, but negatively affected the abundance of seed and grape eaters (Figures 2 and 4). Landscape compositional heterogeneity (i.e. landscape diversity) had a positive effect on taxonomic diversity and the abundance of the three bird functions (Figures 2 and 3). Moreover, landscape diversity increased bird functional evenness and abundance of habitat generalists only in organic vineyards (Figure 2; Appendix S6). Landscape configurational heterogeneity (i.e. edge length) significantly increased functional divergence and evenness, functional insectivores, habitat generalists and song attractiveness (Figure 5). Finally, the effect of organic viticulture also depended on landscape configuration for seed and grape eaters (Figure 2).

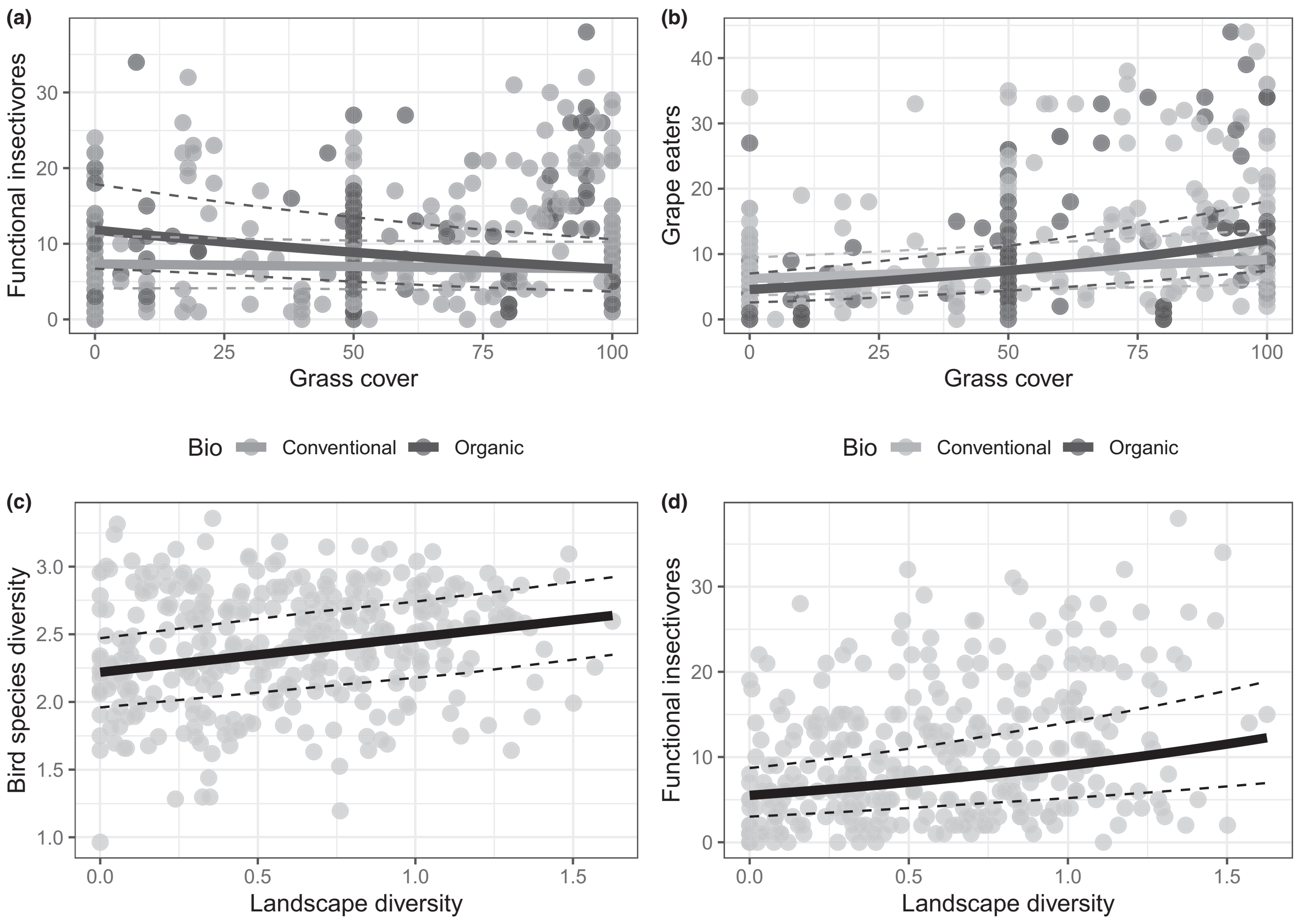

FIGURE 3 Effects of organic management, grass cover and landscape diversity (i.e. compositional heterogeneity) on bird community metrics and individual functions. See Figure 2 for predictor estimates and confidence intervals

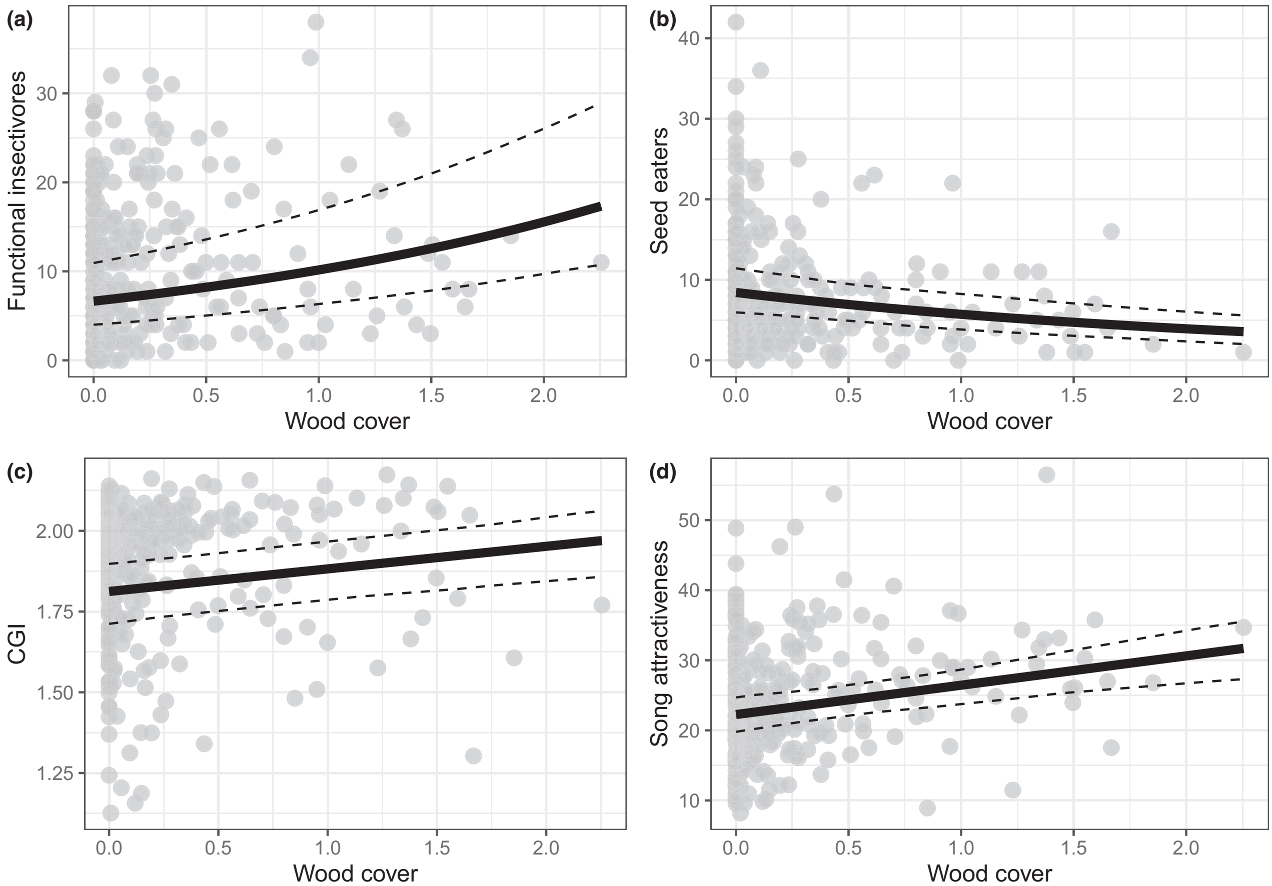

FIGURE 4 Effects of woodland cover on bird community metrics and individual functions. See Figure 2 for predictor estimates and confidence intervals

4 | DISCUSSION

In the present work, we showed that landscape heterogeneity and field-level management jointly contribute, and interact, to shape vineyard bird communities. By simultaneously assessing the effects of organic farming, grass cover management and landscape heterogeneity, we highlighted their combined effects on the conservation of multiple bird functions in European vineyards, to account for multifaceted responses of bird communities to wine farming systems. We found that landscape heterogeneity (both compositional and configurational) was especially important for bird communities, and benefited most bird functional groups, taxonomic diversity and cultural significance. Organic management enhanced both functional diversity and the abundance of insectivorous birds without affecting significantly taxonomic diversity. Moreover, organic farming interacted with (a) inter-row grass cover to drive abundance of functional insectivores, potential grape consumers and seed eaters; and (b) landscape heterogeneity to increase bird functional evenness and the abundance of habitat generalists.

Organic management is not always sufficient to increase biodiversity in farmland, and its effect depends on the taxa, the spatial scale and the landscape considered (Fuller et al., 2005; Gabriel et al., 2010). The positive effect of organic management on species richness and abundance of most taxa is particularly noticeable in homogeneous agricultural landscapes (Tuck et al., 2014). Birds are known to benefit from organic farming, both from grass cover management and release from synthetic pesticides that increase insect and weed resources at local and landscape levels (Fuller et al., 2005; Rollan et al., 2019). However, several studies have not found significant effects of organic vineyard management on birds (Assandri et al., 2016; Puig-Montserrat et al., 2017), likely because organic farming interact with both finer and larger-scale drivers (Gabriel et al., 2010). Pests and diseases affecting grape production differ among wine-growing regions, resulting in different levels of insecticide and fungicide uses in both organic and conventional vineyards (Paredes et al., 2021). At the larger scale investigated here, it was not possible to homogeneously collect information about potential differences in management beyond the 'organic versus non-organic' dichotomy. In particular, the use of copper and sulphur fungicides is still allowed in organic vineyards, and this may locally have additional—and unnoticed—detrimental effects on soil biodiversity, for example on earthworms and other below-ground prey available for ground-probing birds (Barbaro et al., 2019). Tillage intensity (i.e. ploughing depth or frequency) also influence vegetation community and weed diversity, with cascading effects on key food resources for insectivorous and seed-eating birds (Bosco et al., 2019; Duarte

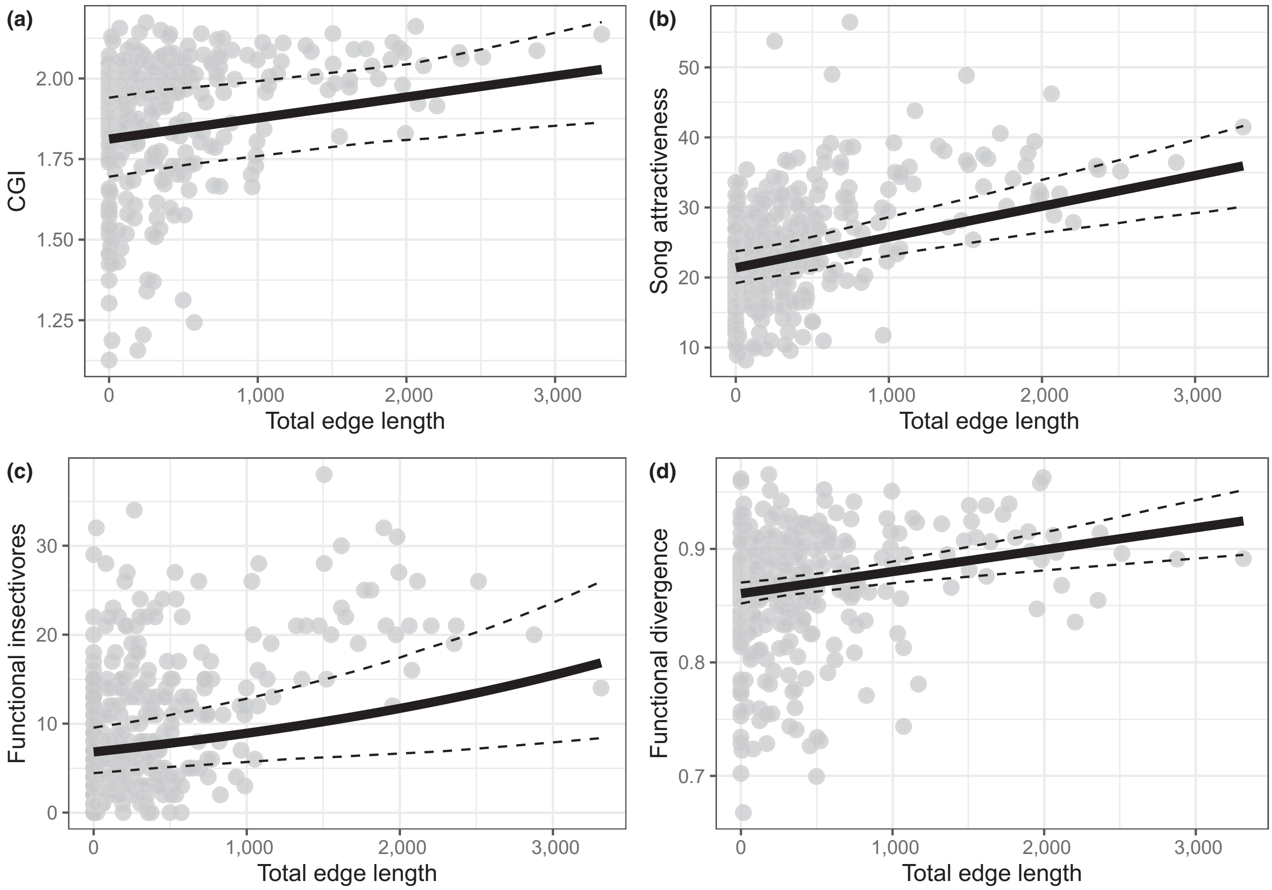

FIGURE 5 Effects of total edge length between vineyards and semi-natural habitats (i.e. landscape configurational heterogeneity) on bird community metrics and individual functions. See Figure 2 for predictor estimates and confidence intervals

et al., 2014). While our approach was relevant to define the shared determinants of vineyard bird communities across different regions, it was not suited to identify region-specific patterns related to environmental or management specificities beyond local gradients of landscape heterogeneity and management intensity. This suggests that future research should focus on region-specific effects of vineyard management on local bird communities, especially regarding species of conservation concern.

Here, by gathering bird data obtained from a broad geographical scale in Europe, we show that the functional diversity of bird communities, and the abundance of target individual functions, are enhanced in vineyard stands conducted under organic management. Moreover, the effect of organic viticulture was contingent upon both field-level management (i.e. grass cover in vine inter-rows) and landscape compositional and configurational heterogeneity. Organic farming benefits are thus enhanced by higher diversity and interspersion of semi-natural habitat patches in the landscape (Assandri et al., 2016; Rollan et al., 2019). Our results suggest that it is critical to also maintain a significant proportion of native vegetation within and between organic vineyards to integrate production and conservation efforts in sustainable viticulture (Froidevaux et al., 2017; Muñoz-Sáez et al., 2020). Management options mixing organic farming at the stand level and maintenance of semi-natural cover in the landscape are not only profitable to birds of conservation concern (Arlettaz et al., 2012; Brambilla, Gustin, et al., 2017), but also to the diversity of avian functions (Assandri et al., 2016; Barbaro et al., 2017; Lourenço et al., 2021). In particular, applying a partial grass cover in vine ranks within organic stands is of particular interest and benefit endangered birds as well as functional diversity (Guyot et al., 2017; Rollan et al., 2019).

However, we also found an unexpected negative effect of grass cover on seed eaters, possibly because many grass covers are too intensively managed to have enough seeds available for specialist granivores such as buntings or finches. Alternatively, uniform grass cover over the entire vineyards might decrease seed detectability for birds, which is likely to be higher in heterogeneous contexts, that is, with patches of bare ground or low-density vegetation. Manipulating grass cover in vine rows also allows the abundance of potential grape-eating birds such as starlings or turdids to be managed, as such ground-probing foragers are more favoured by a full than a partial grass cover. Conserving biodiversity in vineyards has overall positive functional consequences for wine production by providing regulating services of natural pest control (Muneret et al., 2019). Such services might be considered as a biotic insurance against an expected increase in pest insect damage to vineyards with global change, through the diversity of bird functions and functional insectivory (Pejchar et al., 2018). How such a biotic insurance cascades on other ecosystem services remains to be investigated, and particularly how conserving a diversity of bird functions also benefit human well-being. Our study demonstrates the interest of using new, exploratory indices of bird cultural significance, such as song or visual attractiveness, in studies of bird responses to vineyard management (Blackburn et al., 2014; Brambilla, Ilahiane, et al., 2017).

Beyond field-level variables, the amount of semi-natural habitats in the surrounding landscape is a key factor for bird communities in vineyards (Assandri et al., 2016; Guyot et al., 2017; Pithon et al., 2016). Woodland cover increased the abundance of functional, often generalist insectivores with high song attractiveness to humans, but decreased the abundance of seed and grape eaters. In contrast, species of conservation concern, such as Woodlark *Lullula arborea* and Ortolan Bunting *Emberiza hortulana*, two among the most characteristic species of vineyard landscapes, strongly benefit from a combination of stand and landscape-level heterogeneity (Arlettaz et al., 2012; Bosco et al., 2019; Brambilla, Gustin, et al., 2017). Interestingly, we found that both configurational and compositional landscape heterogeneity were important for the conservation of functionally diverse bird communities in vineyards, as predicted by ecological theory (Fahrig et al., 2011). Such positive responses to heterogeneity are due to higher spatial complexity in mosaic landscapes, enhancing positive edge effects on insectivorous birds and their functional diversity, and allowing more complementation processes and spill-over movements between vineyards and adjacent semi-natural habitats (Barbaro et al., 2017; Muñoz-Sáez et al., 2020). Overall, landscape heterogeneity had a positive effect on taxonomic diversity and allowed the coexistence of multiple avian functions in vineyard landscapes. It is likely that such heterogeneity would also benefit other functionally significant taxa allowing pest regulation while contributing to vineyard biodiversity (Caprio et al., 2015; Froidevaux et al., 2017; Rodríguez-San Pedro et al., 2019). Interestingly, we found a positive effect of organic viticulture only in landscapes with higher compositional heterogeneity for bird functional evenness and habitat generalists, in contrast with most previous findings (Tuck et al., 2014).

As a result, managing landscape heterogeneity to conserve vineyard-associated birds and their multiple functions is a valuable option not only for wine growers but also for rural societies inhabiting vineyard landscapes with high cultural significance (Assandri et al., 2018). Previous studies have highlighted that the local potential for biocontrol in vineyards was driven by the diversity of natural enemies and trait complementarities among predators of wine pests, and that this potential was narrowly linked to landscape heterogeneity (Muneret et al., 2019; Redhead et al., 2020). Other services provided by biodiversity, such as pollination, are also favoured by the same type of landscape management (Kratschmer et al., 2019), although trade-offs may also occur between services (Brambilla, Ilahiane, et al., 2017). Conserving a significant proportion of semi-natural cover in the landscape is considered necessary if biodiversity is to provide these services, and to maintain functional complementarity across regions, as a spatial insurance against global change (Tscharntke et al., 2012). In addition, there is a need for maintaining a diversity of wine-growing techniques and grape varieties in the wider landscape to mitigate negative effects of climate and land use changes on vineyard biodiversity, together with the development of agroecological practices (Assandri et al., 2018; Hannah et al., 2013).

In conclusion, our study advocates for a combination of organic management, inter-row grass cover and landscape heterogeneity to maintain bird functional diversity and related ecosystem functions and services in vineyards. Our analyses would further benefit from a more detailed description of actual farming practices used in organic versus non-organic wine farming systems across European regions. Highlighting which practices, beyond the organic versus non-organic dichotomy, are precisely responsible for the effects of organic farming on regional biodiversity across Europe is now of major importance. This would help in building regional strategies to design multifunctional landscapes aiming to conciliate biodiversity conservation and wine production. In other words, vineyards need biodiversity to cope with global change and contribute to the conservation of associated bird communities under Mediterranean-type climates (Muñoz-Sáez et al., 2020; Paiola et al., 2020). A further step would be now to assess how the spatial expansion of agroecological farming practices in interaction with semi-natural habitats is affecting bundles of ecosystem functions and services in European vineyards, including cultural significance or aesthetic values.

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AUTHORS' CONTRIBUTIONS

L.B., G.A., M.B., B.C., B.G., J.P., C.S. and A.R. conceived the study; L.B., G.A., M.B., B.G., J.P., X.P.-M., I.T., P.G., J.G., F.-X.M.-V., S.M., L.R. and A.R. collected and/or provided the data; L.B., B.C., J.F., F.C., P.G. and A.R. computed the metrics, analysed the data and drew the figures; L.B. led the writing and all authors revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.0cfxpnw1p (Barbaro et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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