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Organic management and landscape heterogeneity sustain multiple bird functions in European vineyards

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Wine-growing landscapes host a large diversity of bird functions enhanced by a combination of organic management and landscape heterogeneity

(140 characters)

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Abstract

Conserving functionally diverse bird communities in European farmland is becoming critical, with no exception for the regions of wine production. Management intensification combined with the loss of semi-natural habitats in wine-growing landscapes led to a long-term decline in birds of conservation concern, but also in once common insectivores and seed eaters. We investigated whether organic farming, inter-row grass management and landscape heterogeneity affected multiple bird functions in European vineyards. We analyzed taxonomic and functional diversity of 334 bird communities covering 12 vineyard regions of the three main wine-producing European countries (France, Italy and Spain). We found that organic management enhanced bird functional diversity but that its positive effect on bird functional groups depended on grass cover in vine inter-rows. For several bird functions, the positive effect of organic farming increased with landscape heterogeneity. Forest cover and landscape compositional heterogeneity increased both taxonomic and functional diversity of bird communities, especially functional insectivory. Landscape configurational heterogeneity also increased functional diversity and cultural significance, measured by song attractiveness of bird communities. However, mean bird specialization decreased with forest cover and configurational heterogeneity, meaning that open habitat specialists preferred open landscapes with large vineyard stands. Overall, both bird diversity and functions were enhanced by higher landscape heterogeneity and longer edges between vineyards and semi-natural habitats. Our study highlights the benefits of combining organic management and partial grass cover at the field level and maintenance of interfaces with semi-natural habitats at the landscape level to conserve multifunctional bird communities across European vineyards.

(247 words)

Introduction

Intensification of agricultural practices during the last decades has caused deep changes in bird communities worldwide, threatening endangered species as well as the provision of pest control or seed dispersal by major avian guilds (Bowler et al. 2019; Hendershot et al. 2020). The interplay between farming practices and landscape structure in farmland can mitigate, improve or dampen the synergies between multiple ecosystem functions and services provided by biodiversity (Martin et al. 2019), including those provided by birds (Pejchar et al. 2018). Viticulture is of major economic importance in Europe and currently faces important environmental issues that lead wine growers to shift towards more environmentally friendly management, including agroecological practices such as organic management or use of permanent grass cover (Merot et al. 2019; Paiola et al. 2020). 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 structure 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, European vineyards recently experienced a loss of landscape complexity under the combined effects of land use and climate changes, together with the use of agrochemicals and changes in soil management (Paiola et al. 2020). Landscape heterogeneity is a key driver of biodiversity dynamics in agricultural landscapes (Fahrig et al. 2011), and is of critical importance for the provision of multiple ecological functions and services, such as natural pest control delivered by multiple organisms (Winqvist et al. 2011). In vineyards, landscape diversity allows maintaining ecological functions provided by vertebrate insectivores such as bats and birds (Jedlicka et al. 2011; Assandri et al. 2016; Froidevaux et al. 2017; Rodriguez-San Pedro et al. 2019). Surprisingly, the conservation of vineyard bird communities has received little attention in Europe, mainly because vineyards are often considered as species-poor agroecosystems (Brambilla & Ronchi 2020). However, vineyards have historically supported, and can still potentially host typical bird assemblages including threatened specialists such as lesser grey shrike *Lanius minor* or ortolan bunting *Emberiza hortulana*, now extirpated from most of these formerly used habitats (Isenmann & Debout 2000; Sierro & Arlettaz 2003; Brambilla et al. 2017a). 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 (Pithon et al. 2016; Casas et al. 2020). More generally, the long-term decline of insectivorous birds in vineyards, as in other farmland, is directly related to the loss of semi-natural grasslands and crop intensification (Bowler et al. 2019, Hendershot et al. 2020). Birds provide multiple functions to agriculture and society, including biological control of insects and weeds, as well as cultural values (Cumming & Maciejewski 2017; Pejchar et al. 2018; Brambilla & Ronchi 2020). As a result, conserving functionally diverse bird assemblages in vineyards is becoming more and more critical, given the social and economic importance of this permanent crop production under Mediterranean-type climates (Muñoz-Sáez et al. 2020a; Paiola et al. 2020).

Such bird assemblages are highly dependent on multi-level habitat heterogeneity, both through sward management at the stand level creating various conditions of grass and bare ground cover (Duarte et al. 2014; Bosco et al. 2019) and habitat diversity at the landscape level (Assandri et al. 2016; Muñoz-Sáez et al. 2020b). At the stand level, organic farming or extensive grass cover management should benefit bird communities through higher availability of food resources (higher abundance and diversity of weeds and arthropods) or nesting sites (Fuller et al. 2005; Winqvist et al. 2011). At the landscape scale, higher habitat heterogeneity should benefit bird communities through complementation or supplementation processes between key resources in the landscape (Dunning et al. 1992). The interplay between compositional and configurational landscape heterogeneity should modulate the effects of management practices at the stand level on bird communities, as found for other taxa or ecological functions (Tscharntke et al. 2012; Martin et al. 2019). Following such hypothesis, the local effect of potentially beneficial management for birds, such as organic farming or extensive grass cover management, should be maximal in more intensive landscapes compared to heterogeneous mosaics where bird communities are already diverse due to higher resource availability and habitat diversity (Tuck et al. 2014). The effects of organic farming for vineyard biodiversity is still seldom studied although organic vineyards are rapidly expanding in some countries such as France, Italy or Spain (Assandri et al. 2016; Muneret et al. 2019; Rollan et al. 2019). So far, most studies did not demonstrate a direct and consistent positive effect of organic farming on insectivorous birds or bats. Instead, several studies did report interacting effects of organic farming with grass cover, landscape composition and availability of arthropod prey (Froidevaux et al. 2017; Winter et al. 2018; Rodriguez-San Pedro et al. 2019). As studies on organic farming have shown a wide diversity of effects, we aimed here at exploring its interactions with other practices across a large range of wine-producing regions and landscapes, for a better understanding of the contribution of different management actions to vineyard bird diversity.

We hypothesized that the link between bird communities and vineyard habitats depends on the interaction between field-level management, including organic farming, and type, amount and spatial configuration of surrounding semi-natural habitats. We built a multi-regional dataset on vineyard bird communities from different wine-producing regions of southern Europe to test how the different components of bird communities display consistent and complementary responses to vineyard management and landscape heterogeneity across a wide biogeographic range. We computed a set of multiple community metrics to assess the effects of viticulture on birds as well as the effects of birds on viticulture, by integrating diversity metrics and functional measures, including trait diversity. We predicted that: (i) the effect of organic farming on bird communities would be stronger on bird functional than taxonomic diversity because of wider niche opportunities offered by organic practices, and would interact with both inter-row management and landscape heterogeneity; (ii) the effects of landscape composition and diversity would be more important than vineyard management for bird species diversity and the abundance of functional insectivores, by filtering the regional species pool able to use vineyards at the local scale; and (iii) the effects of landscape configurational heterogeneity would be especially detectable on bird functional diversity and individual avian functions because it would primarily affect bird foraging opportunities by increasing complementation between vineyards and the wider landscape.

Methods

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; Fig. 1). The proportion of organic vs conventional management and the extent of landscape complexity gradient covered varied among regions (Appendix S1). In each region, sites were selected along a landscape composition 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; see Puig-Montserrat et al. 2017). The proportion of organic stands was 31% in the overall dataset (N = 103 vs N = 231 for conventional stands; see Appendix S1). We also measured the proportion of grass cover in vine inter-rows, ranging between 100% (homogeneous grass cover within the entire stand), 50% (partial grass cover due to soil tillage in half of inter-rows) and 0% (bare ground over all the inter-rows). The mean grass cover over the 334 plots was 52% (see Appendix S1), and the distribution of continuous values of grass cover was well balanced between 0 and 100%.

Bird sampling

Bird communities were sampled in different years according to the study region, from 2010 to 2018, but 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 S1). 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 (Appendix S1). 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 (6.00 to 10.00 am) 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 (Appendix S3).

Bird functions and community metrics

We computed nine community-level metrics, including taxonomic diversity, functional diversity and abundance-based avian functions. To account for both species abundance and richness of bird communities, we used the Shannon index of taxonomic diversity. To characterize individual avian functions within bird communities and analyse responses of bird functional composition beyond usual species diversity, we computed the cumulative abundance for several species groups that potentially benefit viticulture (pest control: functional insectivores FI; weed control: seed eaters SE) or may be considered as vine pests (grape eaters GE). We calculated an 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 at the same time: (i) it is insectivorous during the breeding period; (ii) it predominantly forages by foliage gleaning or by hawking; and (iii) it uses vineyards as breeding and/or foraging habitats (N = 34 species). The abundance of seed eaters SE (N = 17 species) and grape eaters GE (N = 9 species) were calculated similarly (Appendix S3). Seed-eating birds were determined based on their diet preferences during the breeding season using authors' personal trait database (Jeliazkov et al. 2020), while potential grape consumers were established with literature inquiries and completed by expert knowledge based on personal field observations of the authors.

To go beyond individual avian functions, we computed three trait-based functional metrics expected to support the largest diversity of species functions, i.e. functional divergence FDiv, functional evenness FEve and functional entropy Rao's Q (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; see Jeliazkov et al. 2020 and Appendix S3). Functional divergence (FDiv) measures trait abundance distribution within this volume and increases with extreme trait values, functional evenness (FEve) increases with the regularity of trait abundance distribution within the functional space, while Rao's Q measures functional entropy by characterizing species dispersion from the functional space centroid, i.e. indicates a community composed of species functionally different from the mean trait composition (Mouillot et al. 2013).

Following Blackburn et al. (2014) or Goodness et al. (2016), we considered mean bird song attractiveness to humans as the most effective proxy for bird cultural services, by calculating the number of individual species recording uploaded in XenoCanto.org online database, weighted by geographic range size (XCRw). Bird conservation concern was expressed by mean bird habitat specialization (Community Generalization Index, CGI), which can be considered as one among the main forms of ecological rarity (Godet et al. 2015; Sykes et al. 2020). The Community Generalization Index is the community-weighted mean value of all Species Generalization Indices (SGI) within a given community (Gaüzère et al. 2020). The Species Generalization Index (SGI) is a measure of habitat niche width of a given species, or ecological rarity, and is computed as the coefficient of variation of the species density across 18 habitat classes at national scale and corresponds to the inverse value of the Species Specialization Index (Godet et al. 2015).

Computation of landscape variables

Land cover maps were realized with ArcGIS 10.6 (ESRI, Redlands, CA, USA) for all regions using the following standard nomenclature: forests and hedgerows, grasslands, shrublands, crops, vineyards, orchards, roads, urban areas and bare ground, waters. For France, land cover maps were derived from two sources, the BD Topo version 2 of 2018 (Institut Géographique National IGN) 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 1:2000 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. 2017b); from Assandri et al. (2016) for Trentino; and from a DMAH land cover map of 2005 for Catalonia (Puig-Montserrat et al. 2017). All GIS maps obtained were visually corrected by one trained geomatician for each study area, especially when vineyards were partially overlapping with other land cover types such as wooded elements. For each land cover type, we computed the total and percent cover in circular 100m-radius buffers around all 334 stands and the Shannon diversity index of land cover types (hereafter referred to as 'landscape diversity') as a measure of landscape compositional heterogeneity. We further calculated the total length of interfaces between all vineyard patches and all types of semi-natural habitats (grasslands, shrublands and forests), as a measure of landscape configurational heterogeneity (Fahrig et al. 2011).

Data analysis

We performed a set of generalized linear mixed models of Gaussian, Poisson and quasi-Poisson families (LMMs and GLMMs) to test the relative effects of vineyard management (organic vs conventional), grass cover and landscape structure on nine bird community metrics and individual avian functions computed for 334 bird communities: species diversity SDiv, Community Generalization Index 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 (Fig. 2). LMMs and GLMMs were built in R software v3.6.0 using the 'glmmTMB' package (Brooks et al. 2020). Three community metrics were count data (sum of species abundance for distinct foraging guilds), and therefore we modelled their responses 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 diversity of land-use types) 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 an 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, and found no differences in predictor performance of model AICs (Brooks et al. 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; 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 assumption was 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 ∆AIC<2), and further report the conditional model average estimates. We checked model residuals for spatial autocorrelation using bubble plots and variograms and drawn prediction biplots based on the best and most parsimonious models.

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, we recorded the presence of *Tetrax tetrax, Burhinus oedicnemus, Galerida theklae, Calandrella brachydactyla, Oenanthe hispanica, Sylvia subalpina* and *Emberiza hortulana* (Appendix S3). The abundance of functional insectivores and the functional diversity of birds (both functional divergence and entropy) significantly increased with organic management (Fig. 2). For functional insectivores as well as grape eaters, the positive effect of organic management was contingent upon inter-row grass cover, with reverse patterns (Fig. 3). By contrast, the abundance of seed eaters decreased with grass cover (Fig. 2).

Forest cover significantly increased the abundance of functional insectivores, habitat generalists (i.e., it decreased mean bird specialization) and mean song attractiveness (Fig. 4). On the other hand, forest cover negatively affected the abundance of seed and grape eaters (Fig. 2 and 4). Landscape compositional heterogeneity (i.e. landscape diversity) had a positive effect on taxonomic diversity and the abundance of the three bird guilds (Fig. 2 and 3). Landscape configurational heterogeneity (i.e. edge length between vineyards and semi-natural habitats) significantly increased functional divergence and evenness, abundance of functional insectivores and habitat generalists, and mean song attractiveness (Fig. 5). Finally, we found significant interactions between organic management and landscape diversity for mean bird specialization, functional divergence and functional evenness, and between organic management and edge length for seed and grape eaters (Fig. 2).

Discussion

In the present work, we assessed simultaneously the effects of organic farming, grass cover management and landscape heterogeneity on the conservation of multiple bird functions in European vineyards. To account for multifaceted responses of bird communities to the vineyard agroecosystem, we assessed both taxonomic and functional diversity and a range of avian functions relevant to viticulture. We found that landscape composition and field-level management jointly contribute to shape vineyard bird communities. Landscape heterogeneity (both compositional and configurational) was also 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 species diversity *per se*. Moreover, the influence of organic farming interacted with inter-row grass cover for functional insectivores, potential grape consumers and seed eaters. Organic management also interacted with landscape heterogeneity to increase bird functional diversity and the abundance of habitat generalists, and to decrease the abundance of seed and grape eaters.

It is now widely recognised that organic farming at the field level is not always sufficient to increase biodiversity in farmland, and that its effect depends on the taxa, the spatial scale, the crop type, and the landscape context (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 more homogeneous agricultural landscapes (Tuck et al. 2014). Birds are known to benefit from organic farming, both from sward management and release from pesticides that increases prey availability at both the field and landscape scale (Fuller et al. 2005; Rollan et al. 2019). However, several studies did not detect significant effects of organic vineyard management on birds or other insectivorous vertebrates such as bats (Assandri et al. 2016; Froidevaux et al. 2017; Puig-Montserrat et al. 2017). In vineyards as much as in other farmland landscapes, it is actually expected that organic management would interact with both fine and larger-scales habitat attributes (Gabriel et al. 2010), which may explain the variety of local responses observed in particular studies. 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 functional guilds, 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 the diversity and configuration of semi-natural cover in the landscape (Assandri et al. 2016; Rollan et al. 2019). Our results thus suggest that it is critical to maintain native vegetation within vineyard stands, as well as larger amounts of semi-natural cover – both open and wooded – within the landscape, to integrate production and conservation efforts in sustainable viticulture (Muñoz-Sáez et al. 2020b).

Management options mixing organic farming at the stand level and maintenance of semi-natural cover in the landscape is not only profitable to birds of conservation concern (Sierro & Arlettaz 2003; Brambilla et al. 2017a; Casas et al. 2020), but also to the diversity of bird functional groups (Assandri et al. 2016; Barbaro et al. 2017). The effect of multi-level heterogeneity results into a complex interaction between field- and landscape-level management of vegetation cover likely to optimize ecosystem functions fulfilled by insectivorous vertebrates in vineyards (Froidevaux et al. 2017). In particular, the interaction between organic management and grass cover showed that these two key viticultural practices are intrinsically related, and that applying a partial grass cover in vine ranks in organic stands will benefit endangered birds as well as functional diversity (Arlettaz et al 2012; Rollan et al. 2019). However, we found an unexpected negative effect of grass cover on seed eaters, likely because many grass covers are often too intensively managed to have enough seeds available for specialists 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, i.e. with patches of bare ground or low-density vegetation. Manipulating grass cover in vine rows also allows managing the abundance of potential grape-eating birds such as starlings or turdids, which, as ground probing foragers, are more favoured by a full than a partial grass cover. Like in other crop types, the conservation of biodiversity in vineyards has positive functional consequences for wine production by providing regulating services of natural pest control (Winqvist et al. 2011; 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 (Barbaro et al. 2017; Pejchar et al. 2018). How this effect cascades on other ecosystem services remains to be fully investigated, in particular those related to human well-being. Our study showed that this could be achieved by using new, exploratory indices of bird cultural significance to humans, including wine producers themselves, such as song or visual attractiveness (Blackburn et al. 2014; Goodness et al. 2016; Brambilla & Ronchi 2020).

The amount of semi-natural cover in the surrounding landscape is a key factor for bird communities in vineyards (Assandri et al. 2016; Pithon et al. 2016; Muñoz-Sáez et al. 2020a). 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 benefitted from a combination of stand and landscape-level heterogeneity (Arlettaz et al. 2012; Brambilla et al. 2017a; Bosco et al. 2019). Interestingly, we found that both landscape configurational and compositional 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 fragmentation 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. 2020a). Overall, landscape heterogeneity had a positive effect on taxonomic diversity and allowed the coexistence of multiple avian functions in vineyard landscapes. Furthermore, it is likely that such heterogeneity would also benefit other functionally significant taxa, allowing pest regulation while contributing importantly to vineyard biodiversity (Caprio et al. 2015; Rodriguez-San Pedro et al. 2019). Managing the wider landscape matrix to conserve bird functions is therefore a valuable option for wine growers, as well as for conservationists and human societies inhabiting vineyard landscapes with high cultural significance (Assandri et al. 2018; Muñoz-Sáez et al. 2020b). Previous studies have highlighted that the local potential for biocontrol in vineyards is driven by the diversity of natural enemies and trait complementarities among predators of wine pests, and that this potential is narrowly linked to landscape complexity (Muneret et al. 2019; Rodriguez-San Pedro et al. 2019). 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 et al. 2017b). Conserving a significant proportion of semi-natural cover in the landscape matrix is considered as necessary for biodiversity to provide these services, and to allow maintaining functional complementarity and redundancy 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 in the wider landscape to mitigate negative effects of climate and land use changes on vineyard biodiversity, together with the development of agroecological practices (Hannah et al. 2013; Assandri et al. 2018).

As a conclusion, our study advocates for encouraging a mixture of traditional and innovative practices in vineyard management, and to consider applying these options at multiple levels from the within-stand heterogeneity to the wider landscape. This offers promising strategies for wine growers to adapt their vineyards to global change, while avoiding further management intensification as observed in the last decades, that appeared to be detrimental to both biodiversity and wine production diversity (Merot et al. 2019; Morales-Castilla et al 2020). In other words, vineland, like other farmland, needs biodiversity to cope with global change and contribute to the critical aim of conserving vineyard-associated biodiversity in countries with Mediterranean-type climates (Muñoz-Sáez et al. 2020a; 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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Supporting information

Appendix S1 to S5

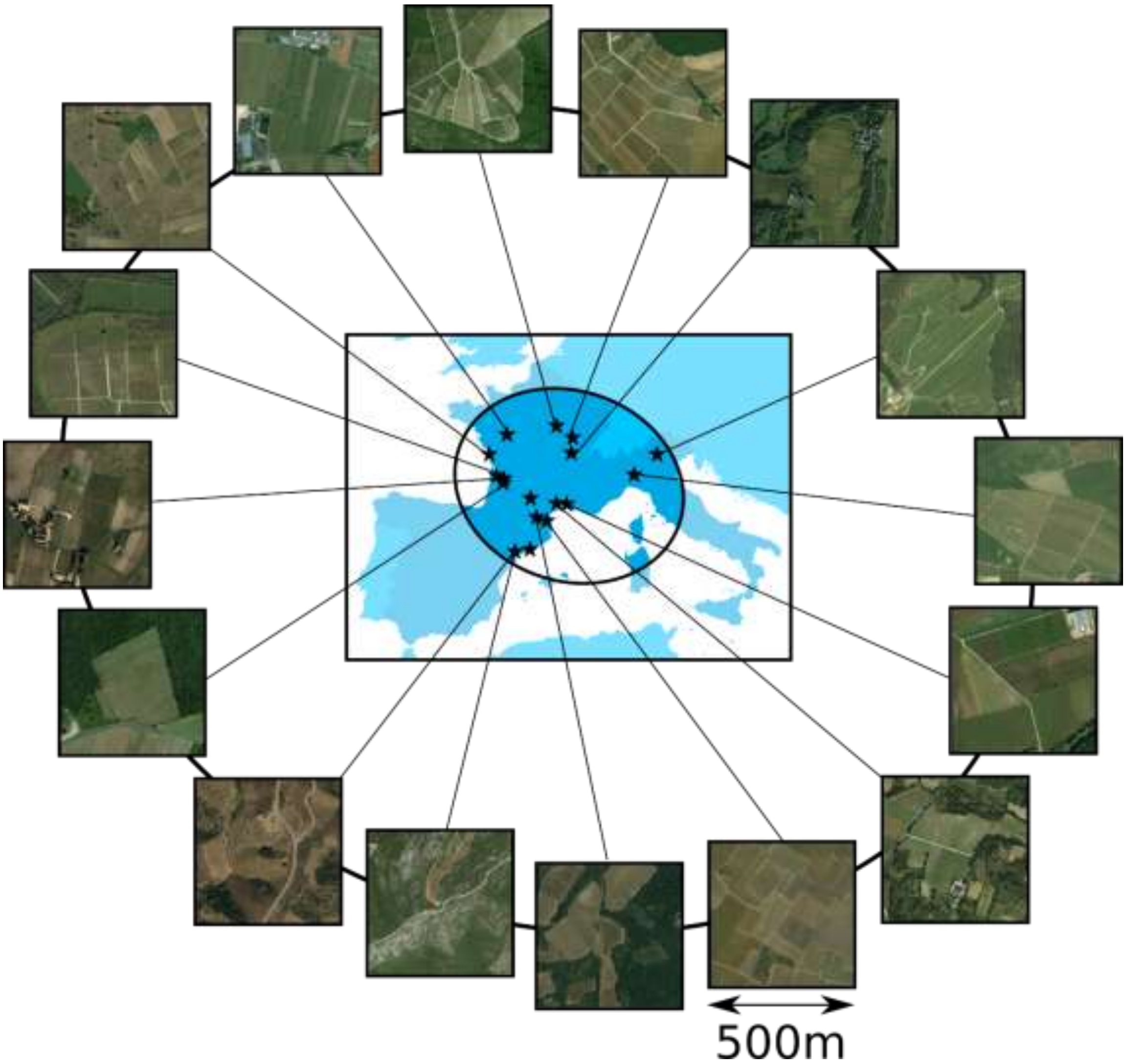

Figure 1. Location map of sampled wine production regions. Clockwise from top: Bourgogne (3 subregions), Trentino, Lombardy (Oltrepo), Costières de Nîmes, Terrasses du Larzac, Corbières, Limoux, Gaillac, Catalunya (2 subregions), Bordeaux (3 subregions: Entre-Deux-Mers, Saint Emilion, Medoc), Ile de Ré, Saumur.

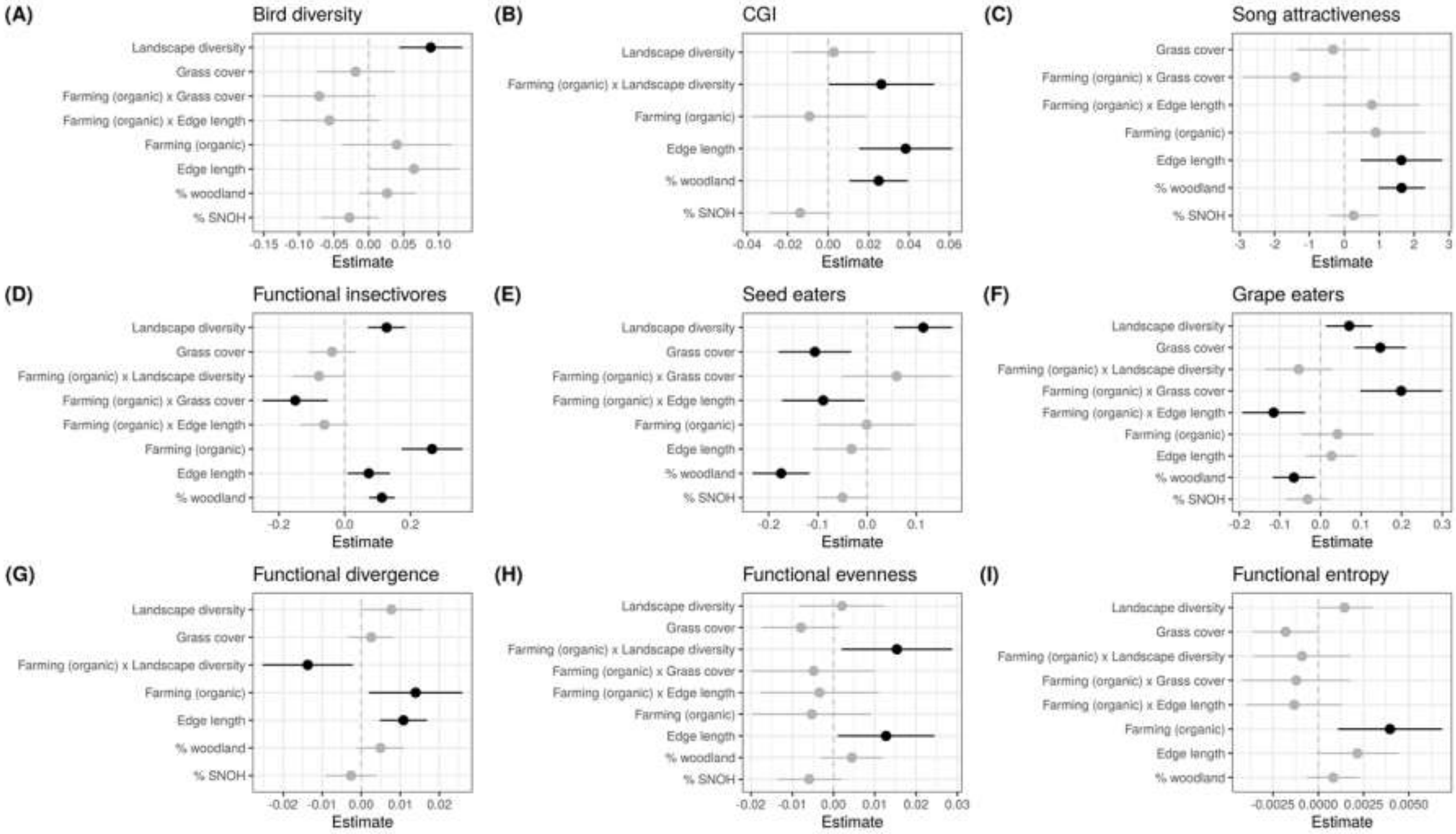

Figure 2. Estimates of conditional averaged models for community metrics, avian functions and functional diversity.

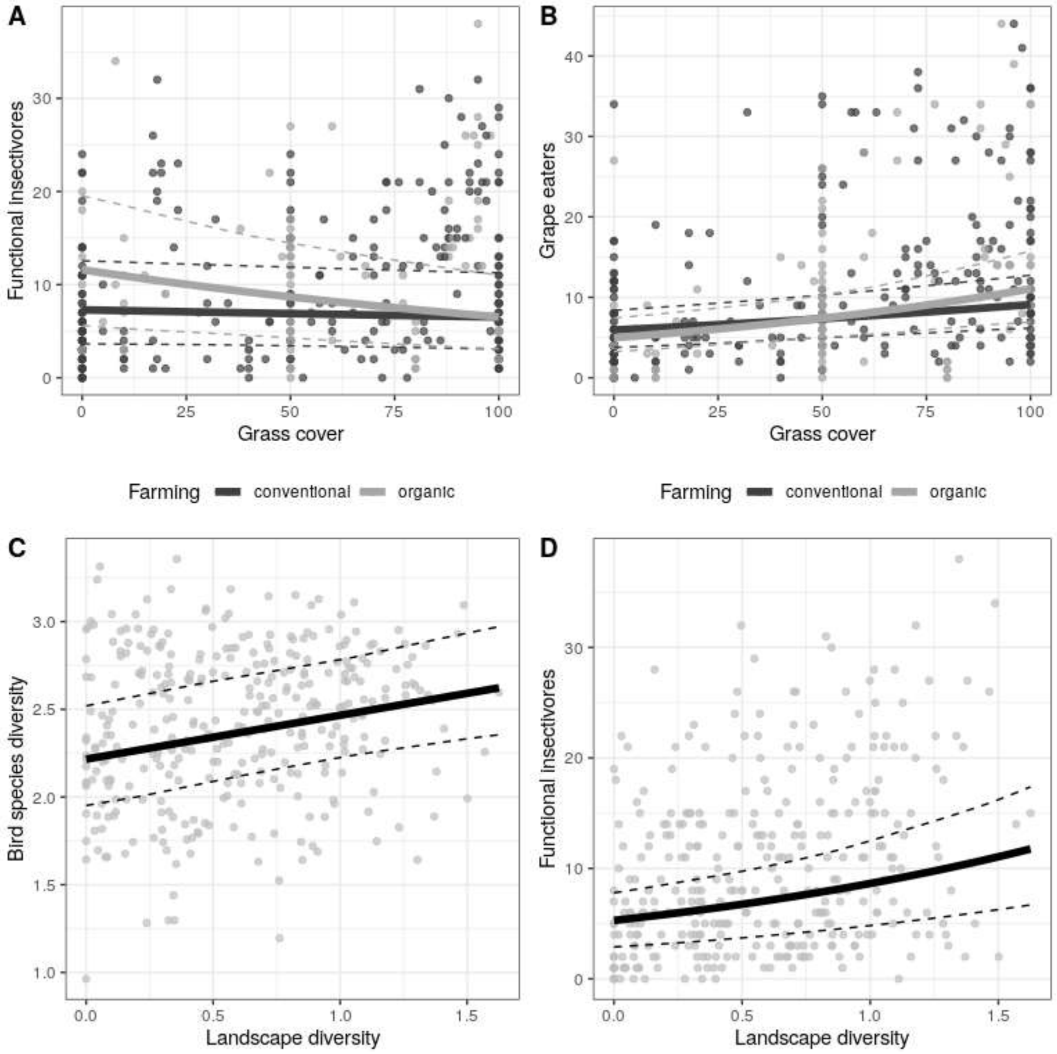

Figure 3. Effects of grass cover and landscape diversity on bird diversity and functions. See Fig. 2 for estimates and confidence intervals.

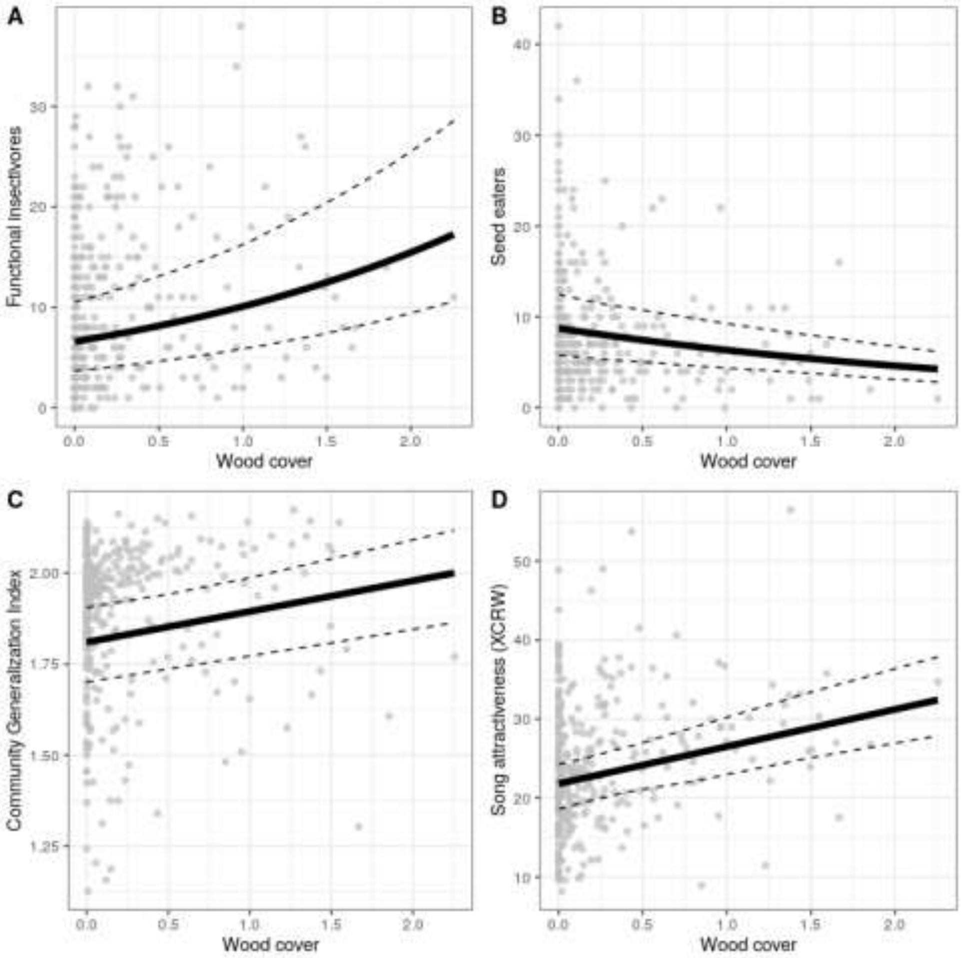

Figure 4. Effects of woodland cover on bird community metrics. See Fig. 2 for estimates and confidence intervals.

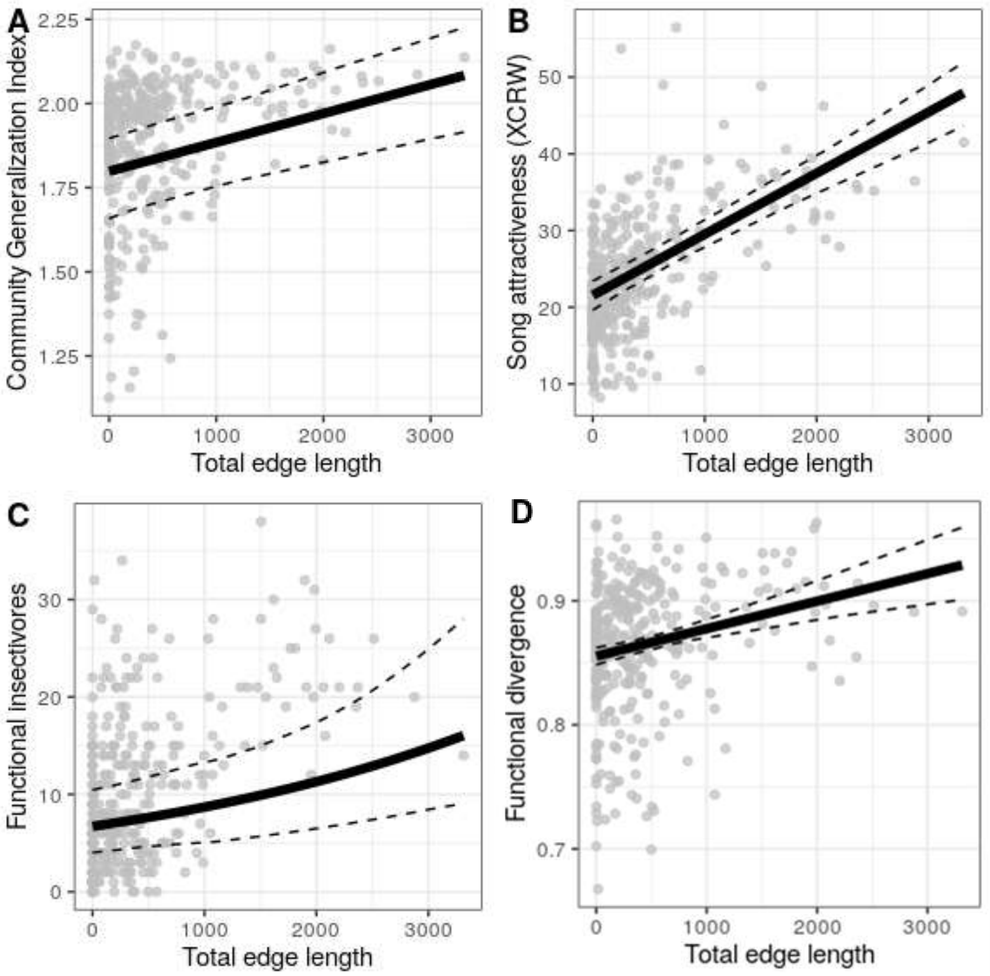

Figure 5. Effects of landscape configurational heterogeneity (edge length between vineyards and semi-natural habitats) on bird community metrics. . See Fig. 2 for estimates and confidence intervals.

Appendix S1. Description of the 12 sampled regions of wine production and study areas

Overall, the bioclimatic variation between wine production areas can be summarized as follows: (i) the northern part lies under more humid oceanic or semi-continental type climates and a mixture of limestones and alluvial soils (graves) where management has been traditionally very intensive and is now more and more organic with increasing use of full or partial inter-row grass cover (60% of vine inter-rows on average); (ii) the eastern part has a more continental climate and is managed intensively, although organic management is also rapidly developing, with increasing use of grass cover (75% on average); and (iii) the southern part has a large diversity of soils on limestones, schists or alluvial deposits under a dry and warm Mediterranean climate. The latter region is the less intensive where organic management is developing rapidly, while vine inter-rows are often kept as bare ground to avoid water competition with grapes (23% of grass cover on average).

The Bourgogne wine growing area extends to 190 000ha, including 25 000ha of AOC (Appelation d'Origine Contrôlée) vineyards, with a wide diversity of landscapes and climates. Vineyards are mainly concentrated in the plains and on the hillsides (12% of the total area) and interspersed with forests on the top of hills (50% of the total area) and cereal and other crops within the landscape mosaic. The climate is mainly oceanic to semi-continental, and the area is characterized by a low altitude variation (from 200 to 500m a.s.l) and limestone soils. In Saumur, part of the Loire Valley vineyards, the study area covered 5900 ha corresponding to the Saumur-Champigny wine production area (protected geographical indication, 'AOC'), of which 1600 ha were vineyards managed by around 120 viticulturists. The area is located on a low elevation limestone plateau submitted to an oceanic to semi-continental climate. Within this area, twelve 1 km square landscape units were selected to represent contexts varying in the proportion of vineyard cover, woodland, crops, built-up land and semi-natural areas (see Pithon et al. 2016 for more details).

The Ile de Ré wine production area covers 650 ha on the third main Atlantic coast island of western France. Ile de Ré vineyards are part of the Cognac production area and are established on sandy soils and maritime alluvions covering a limestone substrate, under an oceanic climate. Vineyards are interspersed with semi-natural grasslands, wetlands and pine forests, with a predominance of organic management. In Bordeaux, the study area is part of Nouvelle Aquitaine region, southwestern France, with a wine production currently covering 145 000 ha of vineyards. In Bordeaux, we sampled three subregions, namely Médoc (Margaux 'AOC' – 1500 ha), Saint Emilion (8000 ha) and Entre-Deux-Mers (1400 ha). The climate is oceanic but the soils are on quaternary alluvial deposits ('graves') in Medoc while they are located on silty and sandy limestones in Saint Emilion and Entre-Deux-Mers, at low elevations between 3 and 107 m a.s.l. In the three subregions, vineyards were selected along a landscape heterogeneity gradient based on the proportion of semi-natural habitats, including both woodlands and semi-natural grasslands.

The Gaillac area is located in southern France, in the Tarn district, where climate is between Oceanic and Mediterranean and the altitude is low, from 105 to 288 m a.s.l. The wine growing region covers 8000 ha, with 2800 ha included in an AOC. Vineyards occur on sedimentary soils in the Tarn valley, in the East hillsides and the Cordes plateau. The study area included 17 vineyards along a landscape complexity gradient of SNH habitat cover, and about half of the stands are managed by organic farming. The Limoux area is located south of Carcassonne in Aude district, at the border between oceanic and Mediterranean climatic influences in southern France. The wine production area extends to 41150 ha from 150 m a.s.l to higher slopes of 750 m a.s.l. The selected area extends to 7800 ha, with two main land uses: forests (25%) and vineyards (26%).

Costières de Nîmes is an area situated in Gard district in southern France, close to the Mediterranean coast. The wine production area extends to 86291 ha at low elevations, from 80 to 100 m a.s.l. The sampled area include 4500 ha mainly composed of vineyards in steady slopes and in open areas, orchards and permanent crops. In the Terrasses du Larzac, the study area is located north-west of Montpellier not far from the Mediterranean coast and the mean altitude is low, lying between 57 and 320 m a.s.l. Climate is Mediterranean and the sampled area extends to 459 ha and gather more than 80 cellars. For the study, 18 vineyards were selected among which 8 were organic. The Roussillon area covers a total area of 15600 ha located in the extreme south of France, under a warm and dry Mediterranean climate. Vineyards are established on various soils depending on topography: limestone slopes (southern Corbières), quaternary alluvial deposits ('graves' of Rivesaltes) and schists (Banyuls).

In Catalonia (Spain), there were two subregions sampled, the first one being in Penedès, in the Mediterranean coast of Spain, a large area of 15000 ha of vineyards (representing 80% of the cultivated area) and other crops such as cereals. It sits in a Tertiary sedimentary depression with a predominantly flat relieve and elevations below 250 m.a.s.l, and has seen in the last decades an intensification of the agricultural practices. The second one was in the Priorat Appellation of Origin, a wine-producing mountainous area covering ca 18000 ha, of which 1887 ha are covered by vineyards located at a mean elevation of 472 ± 250 m.a.s.l. Both areas have a dry Mediterranean climate influenced by the proximity of the sea (Puig-Montserat et al. 2017).

In North Eastern Italy, in Trentino, the wine production area occurs between 65 m a.s.l and 750 m a.s.l. and covers about 10300 ha, concentrated in the valley bottoms and their hilly sides. Vineyard management is quite intensive and organic farming represented only less than 3% of the production area. In addition, there are two types of vineyard structure: *pergola* is the traditional and predominant one and consist in tall vines supported by a robust structure, while *spalliera* is the most widespread wire arrangement. The Oltrepò Pavese area is located in the southern extreme of Lombardy in the North of Italy, from the Po river (up to 50 m a.s.l) to the Apennines mountains (up to 1724 m a.s.l). The study was conducted on the vineyard belt (from 70 to 500 m a.s.l), which covers about 15000 ha, mostly located on gently sloping hills. The area is dominated by intensively managed vineyards, broadleaved woodlands and heterogeneous farming systems.

Appendix S2. Bird sampling methods used in the 12 sampled wine-growing regions.

Country	Region	N	Sampling year	Sampling method	Width or diameter (m)	Surface area sampled (ha)
France	Bordeaux	60	2013 and 2015	Transects and points	100	4
France	Languedoc	25	2015 and 2018	Transects	100	4
France	Gaillac	17	2017	Transects	100	4
France	Limoux	25	2013	Point counts	200	3
France	Costières	24	2013	Point counts	200	3
France	Bourgogne	24	2013	Point counts	200	3
France	Loire	22	2010	Transects	50	5
Spain	Catalunya	23	2013	Point counts	200	1
Italy	Trentino	46	2015	Transects	200	7
Italy	Lombardy	65	2015	Transects	200	7
France	Ile de Ré	3	2018	Transects	100	4

Appendix S3. Table of species abundance and traits

The 10 most frequent species across all regions were in decreasing order Turdus merula, Serinus serinus, Parus major, Corvus corone (corone/cornix), Sylvia atricapilla, Fringilla coelebs, Sturnus vulgaris, Carduelis carduelis, Lullula arborea and Columba palumbus (see Appendix SX).

TBC

Appendix S4. List of species used to calculate the abundance of functional insectivores, seed and grape eaters (see methods).

TBC

Functional insectivores (N = 34 species)

AEGCAU
CISJUN
CLAGLA
CUCCAN
ERIRUB
FICHYP
FRICOE
HIPICT
HIPPOL
LUSMEG
MUSSTR
PARCAE
PARMAJ
PHOOCH
PHOPHO
PHYBON
PHYCOL
PHYLUS
PHYSIB
PRUMOD
REGIGN
REGREG
SAXRUB
SAXTOR
SYLATR
SYLBOR
SYLCAN
SYLCOM
SYLHOR
SYLMEL
SYLSUB
SYLUND
TROTRO
UPUEPO

Seed eaters (N = 17 species)

ALERUF
CARCAN
CARCAR
CARCHL
COCCOC
COLOEN
COLPAL
COTCOT
EMBCAL
EMBCIA
EMBCIR
EMBCIT
PASMON
PHACOL
SERSER
STRDEC
STRTUR

Grape consumers (N = 9 species)

CORCOR
CORFRU
CORMON
GARGLA
PASDOM
STUVUL
TURMER
TURPHI
TURPIL

Appendix S5. Multi-scale analysis of predicting performance for landscape metrics.

Prior to inclusion of landscape predictors into final models, we used the French dataset (N = 200 plots) to assess the relationship between each landscape variable calculated at different spatial scales (100, 500, 750, 1000m buffer around the sampling sites) and response variables to identify the scale best correlated with most bird community metrics. For the 200 French plots were land use data were fully homogeneous at larger distances around sampled vineyards (Inglada et al. 2018), we also computed the same landscape metrics, both compositional and configurational, for three larger buffer sizes of 500, 750 and 1000 m-radius, respectively. For this subsample of the data set, we ran all the models using the same full model structure as detailed in the Methods section for the full data set, with landscape predictors computed in increasing buffers scales of 100, 500, 750 and 1000 m to test their performances and consistencies across larger spatial scales. The best buffer scale selected was always 100 m for all metrics, with a strong consistency in predictor selection, except for species diversity, functional insectivores and functional entropy, for which the best scales were 500 m. However, the same predictors were selected at all scales, except open habitat cover and edge length that has increasing predicting performance with scale at the expense of landscape diversity for functional insectivores.