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1 **Organic management and landscape heterogeneity sustain multiple bird**

2 **functions in European vineyards**

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23

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25

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29

30 **Article impact statement:** In **≤140 characters** (including spaces and punctuation), provide a

31 statement that reveals the paper’s primary importance to conservation. See “Article Impact

32 Statement” below.

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

35 (140 characters)

36

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38

39

40

41

42 **Abstract**

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

63 (247 words)

64 **Introduction**

65 Intensification of agricultural practices during the last decades has caused deep changes in
66 bird communities worldwide, threatening endangered species as well as the provision of pest control
67 or seed dispersal by major avian guilds (Bowler et al. 2019; Hendershot et al. 2020). The interplay
68 between farming practices and landscape structure in farmland can mitigate, improve or dampen the
69 synergies between multiple ecosystem functions and services provided by biodiversity (Martin et al.
70 2019), including those provided by birds (Pejchar et al. 2018). Viticulture is of major economic
71 importance in Europe and currently faces important environmental issues that lead wine growers to
72 shift towards more environmentally friendly management, including agroecological practices such as
73 organic management or use of permanent grass cover (Merot et al. 2019; Paiola et al. 2020). As
74 vineyards are likely to expand more and more at the expense of semi-natural vegetation with climate
75 warming (Hannah et al. 2013), it is critical to better understand the combined effects of field
76 management and landscape structure on bird diversity across a large range of wine production areas.

77 In Europe, vineyards are managed with various intensification levels, but generally result in
78 heterogeneous mosaics of semi-natural habitats interspersed with large areas of grape dedicated to
79 wine production. However, European vineyards recently experienced a loss of landscape complexity
80 under the combined effects of land use and climate changes, together with the use of agrochemicals
81 and changes in soil management (Paiola et al. 2020). Landscape heterogeneity is a key driver of
82 biodiversity dynamics in agricultural landscapes (Fahrig et al. 2011), and is of critical importance for
83 the provision of multiple ecological functions and services, such as natural pest control delivered by
84 multiple organisms (Winqvist et al. 2011). In vineyards, landscape diversity allows maintaining
85 ecological functions provided by vertebrate insectivores such as bats and birds (Jedlicka et al. 2011;
86 Assandri et al. 2016; Froidevaux et al. 2017; Rodriguez-San Pedro et al. 2019). Surprisingly, the
87 conservation of vineyard bird communities has received little attention in Europe, mainly because
88 vineyards are often considered as species-poor agroecosystems (Brambilla & Ronchi 2020). However,

89 vineyards have historically supported, and can still potentially host typical bird assemblages including
90 threatened specialists such as lesser grey shrike *Lanius minor* or ortolan bunting *Emberiza hortulana*,
91 now extirpated from most of these formerly used habitats (Isenmann & Debout 2000; Siervo &
92 Arlettaz 2003; Brambilla et al. 2017a). Other species of conservation concern, such as great bustard
93 *Otis tarda*, little bustard *Tetrax tetrax* or stone curlew *Burhinus oedicanus*, have also disappeared
94 from most vineyard landscapes following management intensification and may not persist without
95 sufficient scrub/grassland patches in the landscape (Pithon et al. 2016; Casas et al. 2020). More
96 generally, the long-term decline of insectivorous birds in vineyards, as in other farmland, is directly
97 related to the loss of semi-natural grasslands and crop intensification (Bowler et al. 2019, Hendershot
98 et al. 2020). Birds provide multiple functions to agriculture and society, including biological control of
99 insects and weeds, as well as cultural values (Cumming & Maciejewski 2017; Pejchar et al. 2018;
100 Brambilla & Ronchi 2020). As a result, conserving functionally diverse bird assemblages in vineyards
101 is becoming more and more critical, given the social and economic importance of this permanent
102 crop production under Mediterranean-type climates (Muñoz-Sáez et al. 2020a; Paiola et al. 2020).

103 Such bird assemblages are highly dependent on multi-level habitat heterogeneity, both
104 through sward management at the stand level creating various conditions of grass and bare ground
105 cover (Duarte et al. 2014; Bosco et al. 2019) and habitat diversity at the landscape level (Assandri et
106 al. 2016; Muñoz-Sáez et al. 2020b). At the stand level, organic farming or extensive grass cover
107 management should benefit bird communities through higher availability of food resources (higher
108 abundance and diversity of weeds and arthropods) or nesting sites (Fuller et al. 2005; Winqvist et al.
109 2011). At the landscape scale, higher habitat heterogeneity should benefit bird communities through
110 complementation or supplementation processes between key resources in the landscape (Dunning
111 et al. 1992). The interplay between compositional and configurational landscape heterogeneity
112 should modulate the effects of management practices at the stand level on bird communities, as
113 found for other taxa or ecological functions (Tschardt et al. 2012; Martin et al. 2019). Following
114 such hypothesis, the local effect of potentially beneficial management for birds, such as organic

115 farming or extensive grass cover management, should be maximal in more intensive landscapes
116 compared to heterogeneous mosaics where bird communities are already diverse due to higher
117 resource availability and habitat diversity (Tuck et al. 2014). The effects of organic farming for
118 vineyard biodiversity is still seldom studied although organic vineyards are rapidly expanding in some
119 countries such as France, Italy or Spain (Assandri et al. 2016; Muneret et al. 2019; Rollan et al. 2019).
120 So far, most studies did not demonstrate a direct and consistent positive effect of organic farming on
121 insectivorous birds or bats. Instead, several studies did report interacting effects of organic farming
122 with grass cover, landscape composition and availability of arthropod prey (Froidevaux et al. 2017;
123 Winter et al. 2018; Rodriguez-San Pedro et al. 2019). As studies on organic farming have shown a
124 wide diversity of effects, we aimed here at exploring its interactions with other practices across a
125 large range of wine-producing regions and landscapes, for a better understanding of the contribution
126 of different management actions to vineyard bird diversity.

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

141 configurational heterogeneity would be especially detectable on bird functional diversity and
142 individual avian functions because it would primarily affect bird foraging opportunities by increasing
143 complementation between vineyards and the wider landscape.

144

145 **Methods**

146 *Study areas*

147 We studied 12 wine-growing regions located in three countries of southern Europe that are
148 the three main producers of wine worldwide: France (nine regions), Italy (two regions) and Spain
149 (one region; Fig. 1). The proportion of organic vs conventional management and the extent of
150 landscape complexity gradient covered varied among regions (Appendix S1). In each region, sites
151 were selected along a landscape composition gradient based on the proportion of woodlands and
152 semi-natural grasslands in the surrounding landscape. For each stand, we determined the type of
153 management (organic or conventional) by local inquiries combined with information gathered by
154 dedicated professional structures (e.g., DOQP bureau in Spain; see Puig-Montserrat et al. 2017). The
155 proportion of organic stands was 31% in the overall dataset (N = 103 vs N = 231 for conventional
156 stands; see Appendix S1). We also measured the proportion of grass cover in vine inter-rows, ranging
157 between 100% (homogeneous grass cover within the entire stand), 50% (partial grass cover due to
158 soil tillage in half of inter-rows) and 0% (bare ground over all the inter-rows). The mean grass cover
159 over the 334 plots was 52% (see Appendix S1), and the distribution of continuous values of grass
160 cover was well balanced between 0 and 100%.

161

162 *Bird sampling*

163 Bird communities were sampled in different years according to the study region, from 2010
164 to 2018, but 85% (i.e., 285 among the 334 plots) were sampled either in 2013 or 2015, with no bias

165 towards organic or conventional vineyards in a particular year (Appendix S1). Birds were surveyed
166 using point or transect counts by single trained observers per region. All birds heard and seen were
167 recorded (except flyovers), within a distance of 50 to 100 m from the observer on each transect side,
168 depending on the region (Appendix S1). Point counts were performed using a standard distance
169 detection of 100 m. To account for differences in the area sampled between circular points and
170 transect counts, we included the sampled area as a random model predictor. We assumed that
171 variation in species detectability was limited among sampled vineyards due to the highly similar and
172 homogeneous structure of vine rows. Bird counts were performed early in the morning (6.00 to
173 10.00 am) only during days without heavy rain or wind. Bird counts were conducted twice, the first
174 visit between mid-April (early-season breeders) and mid-May and the second visit between late May
175 and mid-June (late-season breeders), except in Italy where a third visit was conducted between these
176 two visits. For each species, the highest count among the two or three visits was further used as a
177 standardized estimate of abundance (Appendix S3).

178

179 *Bird functions and community metrics*

180 We computed nine community-level metrics, including taxonomic diversity, functional
181 diversity and abundance-based avian functions. To account for both species abundance and richness
182 of bird communities, we used the Shannon index of taxonomic diversity. To characterize individual
183 avian functions within bird communities and analyse responses of bird functional composition
184 beyond usual species diversity, we computed the cumulative abundance for several species groups
185 that potentially benefit viticulture (pest control: functional insectivores FI; weed control: seed eaters
186 SE) or may be considered as vine pests (grape eaters GE). We calculated an index of functional
187 insectivory by cumulating the abundance of species sharing a similar combination of diet, foraging
188 technique and habitat use (Barbaro et al. 2017). A bird species was considered a 'functional
189 insectivore' in vineyards when at the same time: (i) it is insectivorous during the breeding period; (ii)

190 it predominantly forages by foliage gleaning or by hawking; and (iii) it uses vineyards as breeding
191 and/or foraging habitats (N = 34 species). The abundance of seed eaters SE (N = 17 species) and
192 grape eaters GE (N = 9 species) were calculated similarly (Appendix S3). Seed-eating birds were
193 determined based on their diet preferences during the breeding season using authors' personal trait
194 database (Jeliazkov et al. 2020), while potential grape consumers were established with literature
195 inquiries and completed by expert knowledge based on personal field observations of the authors.

196 To go beyond individual avian functions, we computed three trait-based functional metrics
197 expected to support the largest diversity of species functions, i.e. functional divergence FDiv,
198 functional evenness FEve and functional entropy Rao's Q (Mouillot et al. 2013). We used a species-
199 trait matrix of eight life-history traits, including six categorical traits (foraging method, adult diet,
200 nesting site, migration strategy, mean laying date and mean home range size) and two continuous
201 traits (clutch size and body mass; see Jeliazkov et al. 2020 and Appendix S3). Functional divergence
202 (FDiv) measures trait abundance distribution within this volume and increases with extreme trait
203 values, functional evenness (FEve) increases with the regularity of trait abundance distribution within
204 the functional space, while Rao's Q measures functional entropy by characterizing species dispersion
205 from the functional space centroid, i.e. indicates a community composed of species functionally
206 different from the mean trait composition (Mouillot et al. 2013).

207 Following Blackburn et al. (2014) or Goodness et al. (2016), we considered mean bird song
208 attractiveness to humans as the most effective proxy for bird cultural services, by calculating the
209 number of individual species recording uploaded in XenoCanto.org online database, weighted by
210 geographic range size (XCRw). Bird conservation concern was expressed by mean bird habitat
211 specialization (Community Generalization Index, CGI), which can be considered as one among the
212 main forms of ecological rarity (Godet et al. 2015; Sykes et al. 2020). The Community Generalization
213 Index is the community-weighted mean value of all Species Generalization Indices (SGI) within a
214 given community (Gaüzère et al. 2020). The Species Generalization Index (SGI) is a measure of

215 habitat niche width of a given species, or ecological rarity, and is computed as the coefficient of
216 variation of the species density across 18 habitat classes at national scale and corresponds to the
217 inverse value of the Species Specialization Index (Godet et al. 2015).

218

219 *Computation of landscape variables*

220 Land cover maps were realized with ArcGIS 10.6 (ESRI, Redlands, CA, USA) for all regions
221 using the following standard nomenclature: forests and hedgerows, grasslands, shrublands, crops,
222 vineyards, orchards, roads, urban areas and bare ground, waters. For France, land cover maps were
223 derived from two sources, the BD Topo version 2 of 2018 (Institut Géographique National IGN) and
224 the Cesbio OSO2018 online database in vector format downloaded from [http://osr-cesbio.ups-](http://osr-cesbio.ups-tlse.fr/~oso/)
225 [tlse.fr/~oso/](http://osr-cesbio.ups-tlse.fr/~oso/) (Inglada et al. 2018). For Italy and Spain, land cover maps were obtained from photo-
226 interpretation of aerial photographs at 1:2000 combined with pre-established land cover maps using
227 the same nomenclature as above; taken from www.geoportale.regione.lombardia.it for Lombardy
228 (Brambilla et al. 2017b); from Assandri et al. (2016) for Trentino; and from a DMAH land cover map
229 of 2005 for Catalonia (Puig-Montserrat et al. 2017). All GIS maps obtained were visually corrected by
230 one trained geomatician for each study area, especially when vineyards were partially overlapping
231 with other land cover types such as wooded elements. For each land cover type, we computed the
232 total and percent cover in circular 100m-radius buffers around all 334 stands and the Shannon
233 diversity index of land cover types (hereafter referred to as 'landscape diversity') as a measure of
234 landscape compositional heterogeneity. We further calculated the total length of interfaces between
235 all vineyard patches and all types of semi-natural habitats (grasslands, shrublands and forests), as a
236 measure of landscape configurational heterogeneity (Fahrig et al. 2011).

237

238

239 *Data analysis*

240 We performed a set of generalized linear mixed models of Gaussian, Poisson and quasi-
241 Poisson families (LMMs and GLMMs) to test the relative effects of vineyard management (organic vs
242 conventional), grass cover and landscape structure on nine bird community metrics and individual
243 avian functions computed for 334 bird communities: species diversity SDiv, Community
244 Generalization Index CGI, mean song attractiveness XCRw, functional insectivore abundance FI, seed
245 eater abundance SE, grape eater abundance GE, functional divergence FDiv, functional evenness
246 FEve and functional entropy RaoQ (Fig. 2). LMMs and GLMMs were built in R software v3.6.0 using
247 the 'glmmTMB' package (Brooks et al. 2020). Three community metrics were count data (sum of
248 species abundance for distinct foraging guilds), and therefore we modelled their responses using
249 Poisson distribution (FI and GE) or quasi-Poisson (SE) distribution to handle over-dispersion. All other
250 metrics (taxonomic and functional diversity, CGI and XCRw) were modelled using the Gaussian
251 distribution after checking for normality and heteroscedasticity of residuals using Shapiro-Wilk tests.

252 We used the same full model structure for all response variables, including the following
253 fixed effects: the interaction between vineyard management (organic vs conventional) and inter-row
254 grass cover, the interactions between organic management and landscape compositional (Shannon
255 diversity of land-use types) and configurational heterogeneity (length of vineyard – semi-natural
256 habitat edges), and two variables of landscape composition (% of semi-natural open habitats and
257 woodlands). The region of wine production (N = 12) was considered as a random effect to account
258 for spatial gathering of sampled stands, biogeographical differences, and for the combination of year
259 and observer effects. We also included the area sampled as a second, additive random effect to
260 account for differences in sampling protocols among regions. Because we expected an effect of
261 sampling protocol on abundance-based metrics (SDiv, FI, GE and SE), but not on integrative
262 community indices (CGI, FDiv, FEve, Rao's Q and XCRw), we also tested the area sampled as an offset

263 in mixed models structure for bird guilds, and found no differences in predictor performance of
264 model AICs (Brooks et al. 2020).

265 All continuous variables were standardized (i.e., rescaled to the same unit) to enable
266 comparisons of effect magnitude. We evaluated multicollinearity among predictors with both the
267 variance inflation factor (VIF) and the Spearman's correlation test; no strong correlation was found
268 (VIF values < 3; $|r| < 0.6$). Model validation was conducted using the 'DHARMA' package (Hartig 2020).
269 We performed the Shapiro Wilk test on LMMs' residuals to ensure that normality assumption was
270 met. Based on the full models, we generated a set of candidate models containing all possible
271 variable combinations using 'MuMIn' package (Bartoń 2020). We applied an information theoretic
272 approach to assess model parsimony and models were ranked based on their Akaike Information
273 Criterion (AIC). To account for model selection uncertainties, we performed a model-averaged
274 procedure of most parsimonious models (i.e. those with $\Delta AIC < 2$), and further report the conditional
275 model average estimates. We checked model residuals for spatial autocorrelation using bubble plots
276 and variograms and drawn prediction biplots based on the best and most parsimonious models.

277

278 **Results**

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

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

299

300 **Discussion**

301 In the present work, we assessed simultaneously the effects of organic farming, grass cover
302 management and landscape heterogeneity on the conservation of multiple bird functions in
303 European vineyards. To account for multifaceted responses of bird communities to the vineyard
304 agroecosystem, we assessed both taxonomic and functional diversity and a range of avian functions
305 relevant to viticulture. We found that landscape composition and field-level management jointly
306 contribute to shape vineyard bird communities. Landscape heterogeneity (both compositional and
307 configurational) was also important for bird communities, and benefited most bird functional groups,
308 taxonomic diversity and cultural significance. Organic management enhanced both functional
309 diversity and the abundance of insectivorous birds without affecting species diversity *per se*.
310 Moreover, the influence of organic farming interacted with inter-row grass cover for functional
311 insectivores, potential grape consumers and seed eaters. Organic management also interacted with

312 landscape heterogeneity to increase bird functional diversity and the abundance of habitat
313 generalists, and to decrease the abundance of seed and grape eaters.

314 It is now widely recognised that organic farming at the field level is not always sufficient to
315 increase biodiversity in farmland, and that its effect depends on the taxa, the spatial scale, the crop
316 type, and the landscape context (Fuller et al. 2005 ; Gabriel et al. 2010). The positive effect of organic
317 management on species richness and abundance of most taxa is particularly noticeable in more
318 homogeneous agricultural landscapes (Tuck et al. 2014). Birds are known to benefit from organic
319 farming, both from sward management and release from pesticides that increases prey availability at
320 both the field and landscape scale (Fuller et al. 2005; Rollan et al. 2019). However, several studies did
321 not detect significant effects of organic vineyard management on birds or other insectivorous
322 vertebrates such as bats (Assandri et al. 2016; Froidevaux et al. 2017; Puig-Montserrat et al. 2017). In
323 vineyards as much as in other farmland landscapes, it is actually expected that organic management
324 would interact with both fine and larger-scales habitat attributes (Gabriel et al. 2010), which may
325 explain the variety of local responses observed in particular studies. Here, by gathering bird data
326 obtained from a broad geographical scale in Europe, we show that the functional diversity of bird
327 communities, and the abundance of target functional guilds, are enhanced in vineyard stands
328 conducted under organic management. Moreover, the effect of organic viticulture was contingent
329 upon both field-level management (i.e., grass cover in vine inter-rows) and the diversity and
330 configuration of semi-natural cover in the landscape (Assandri et al. 2016; Rollan et al. 2019). Our
331 results thus suggest that it is critical to maintain native vegetation within vineyard stands, as well as
332 larger amounts of semi-natural cover – both open and wooded – within the landscape, to integrate
333 production and conservation efforts in sustainable viticulture (Muñoz-Sáez et al. 2020b).

334 Management options mixing organic farming at the stand level and maintenance of semi-
335 natural cover in the landscape is not only profitable to birds of conservation concern (Sierro &
336 Arlettaz 2003; Brambilla et al. 2017a; Casas et al. 2020), but also to the diversity of bird functional

337 groups (Assandri et al. 2016; Barbaro et al. 2017). The effect of multi-level heterogeneity results into
338 a complex interaction between field- and landscape-level management of vegetation cover likely to
339 optimize ecosystem functions fulfilled by insectivorous vertebrates in vineyards (Froidevaux et al.
340 2017). In particular, the interaction between organic management and grass cover showed that
341 these two key viticultural practices are intrinsically related, and that applying a partial grass cover in
342 vine ranks in organic stands will benefit endangered birds as well as functional diversity (Arlettaz et al
343 2012; Rollan et al. 2019). However, we found an unexpected negative effect of grass cover on seed
344 eaters, likely because many grass covers are often too intensively managed to have enough seeds
345 available for specialists such as buntings or finches. Alternatively, uniform grass cover over the entire
346 vineyards might decrease seed detectability for birds, which is likely to be higher in heterogeneous
347 contexts, i.e. with patches of bare ground or low-density vegetation. Manipulating grass cover in vine
348 rows also allows managing the abundance of potential grape-eating birds such as starlings or turdids,
349 which, as ground probing foragers, are more favoured by a full than a partial grass cover. Like in
350 other crop types, the conservation of biodiversity in vineyards has positive functional consequences
351 for wine production by providing regulating services of natural pest control (Winqvist et al. 2011;
352 Muneret et al. 2019). Such services might be considered as a biotic insurance against an expected
353 increase in pest insect damage to vineyards with global change, through the diversity of bird
354 functions and functional insectivory (Barbaro et al. 2017; Pejchar et al. 2018). How this effect
355 cascades on other ecosystem services remains to be fully investigated, in particular those related to
356 human well-being. Our study showed that this could be achieved by using new, exploratory indices of
357 bird cultural significance to humans, including wine producers themselves, such as song or visual
358 attractiveness (Blackburn et al. 2014; Goodness et al. 2016; Brambilla & Ronchi 2020).

359 The amount of semi-natural cover in the surrounding landscape is a key factor for bird
360 communities in vineyards (Assandri et al. 2016; Pithon et al. 2016; Muñoz-Sáez et al. 2020a).
361 Woodland cover increased the abundance of functional, often generalist insectivores with high song
362 attractiveness to humans, but decreased the abundance of seed and grape eaters. In contrast,

363 species of conservation concern, such as woodlark *Lullula arborea* and ortolan bunting *Emberiza*
364 *hortulana*, two among the most characteristic species of vineyard landscapes, strongly benefitted
365 from a combination of stand and landscape-level heterogeneity (Arlettaz et al. 2012; Brambilla et al.
366 2017a; Bosco et al. 2019). Interestingly, we found that both landscape configurational and
367 compositional heterogeneity were important for the conservation of functionally diverse bird
368 communities in vineyards, as predicted by ecological theory (Fahrig et al. 2011). Such positive
369 responses to fragmentation are due to higher spatial complexity in mosaic landscapes, enhancing
370 positive edge effects on insectivorous birds and their functional diversity, and allowing more
371 complementation processes and spill-over movements between vineyards and adjacent semi-natural
372 habitats (Barbaro et al. 2017; Muñoz-Sáez et al. 2020a). Overall, landscape heterogeneity had a
373 positive effect on taxonomic diversity and allowed the coexistence of multiple avian functions in
374 vineyard landscapes. Furthermore, it is likely that such heterogeneity would also benefit other
375 functionally significant taxa, allowing pest regulation while contributing importantly to vineyard
376 biodiversity (Caprio et al. 2015; Rodriguez-San Pedro et al. 2019). Managing the wider landscape
377 matrix to conserve bird functions is therefore a valuable option for wine growers, as well as for
378 conservationists and human societies inhabiting vineyard landscapes with high cultural significance
379 (Assandri et al. 2018; Muñoz-Sáez et al. 2020b). Previous studies have highlighted that the local
380 potential for biocontrol in vineyards is driven by the diversity of natural enemies and trait
381 complementarities among predators of wine pests, and that this potential is narrowly linked to
382 landscape complexity (Muneret et al. 2019; Rodriguez-San Pedro et al. 2019). Other services
383 provided by biodiversity, such as pollination, are also favoured by the same type of landscape
384 management (Kratschmer et al. 2019), although trade-offs may also occur between services
385 (Brambilla et al. 2017b). Conserving a significant proportion of semi-natural cover in the landscape
386 matrix is considered as necessary for biodiversity to provide these services, and to allow maintaining
387 functional complementarity and redundancy across regions as a spatial insurance against global
388 change (Tscharntke et al. 2012). In addition, there is a need for maintaining a diversity of wine-

389 growing techniques in the wider landscape to mitigate negative effects of climate and land use
390 changes on vineyard biodiversity, together with the development of agroecological practices
391 (Hannah et al. 2013; Assandri et al. 2018).

392 As a conclusion, our study advocates for encouraging a mixture of traditional and innovative
393 practices in vineyard management, and to consider applying these options at multiple levels from the
394 within-stand heterogeneity to the wider landscape. This offers promising strategies for wine growers
395 to adapt their vineyards to global change, while avoiding further management intensification as
396 observed in the last decades, that appeared to be detrimental to both biodiversity and wine
397 production diversity (Merot et al. 2019; Morales-Castilla et al 2020). In other words, vineland, like
398 other farmland, needs biodiversity to cope with global change and contribute to the critical aim of
399 conserving vineyard-associated biodiversity in countries with Mediterranean-type climates (Muñoz-
400 Sáez et al. 2020a; Paiola et al. 2020). A further step would be now to assess how the spatial
401 expansion of agroecological farming practices in interaction with semi-natural habitats is affecting
402 bundles of ecosystem functions and services in European vineyards, including cultural significance or
403 aesthetic values.

404

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533 grant agreement No 311879. This is a contribution to the project LIFE+2009 BioDiVine.

534

535 **Supporting information**

536 **Appendix S1 to S5**

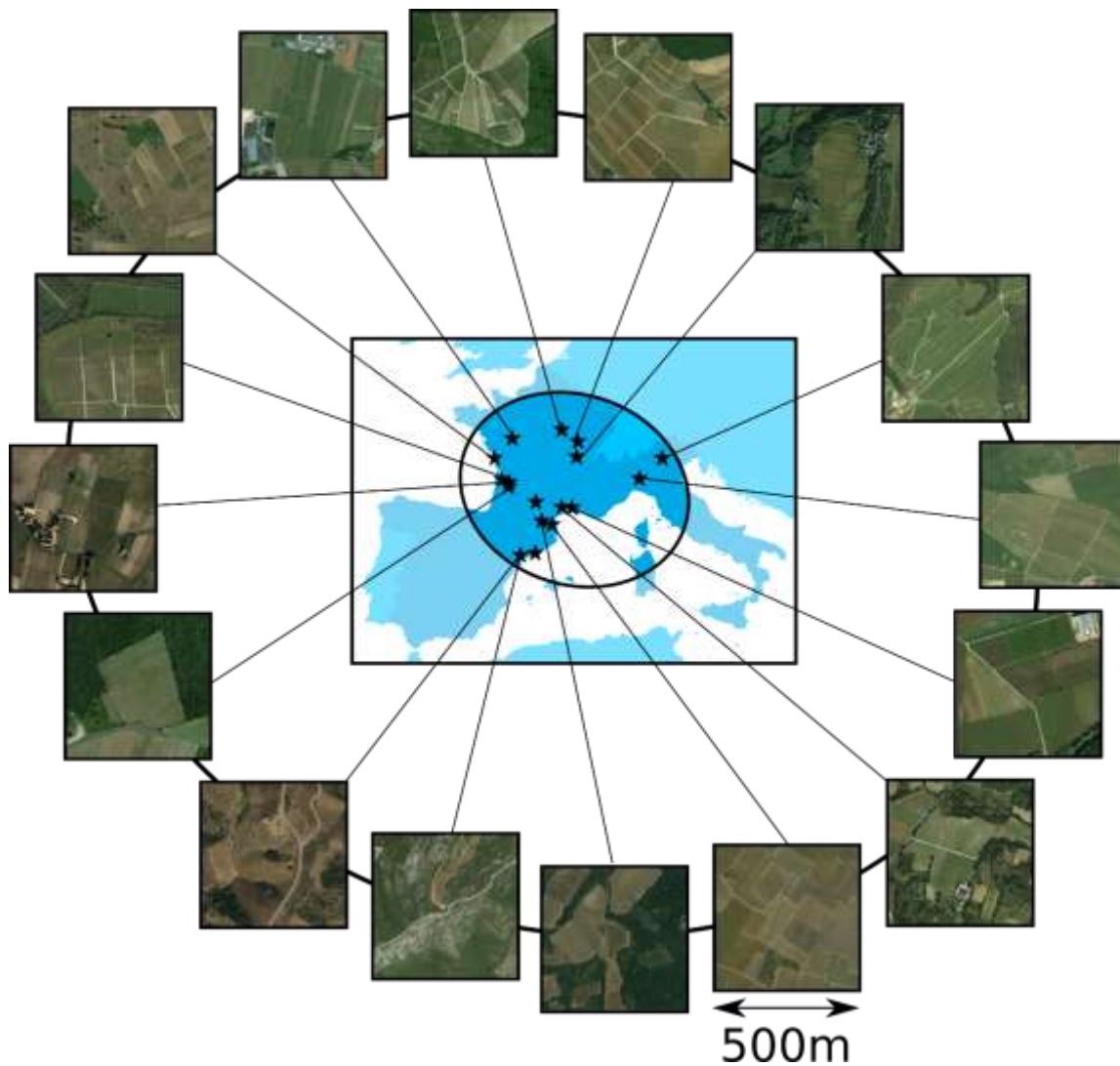
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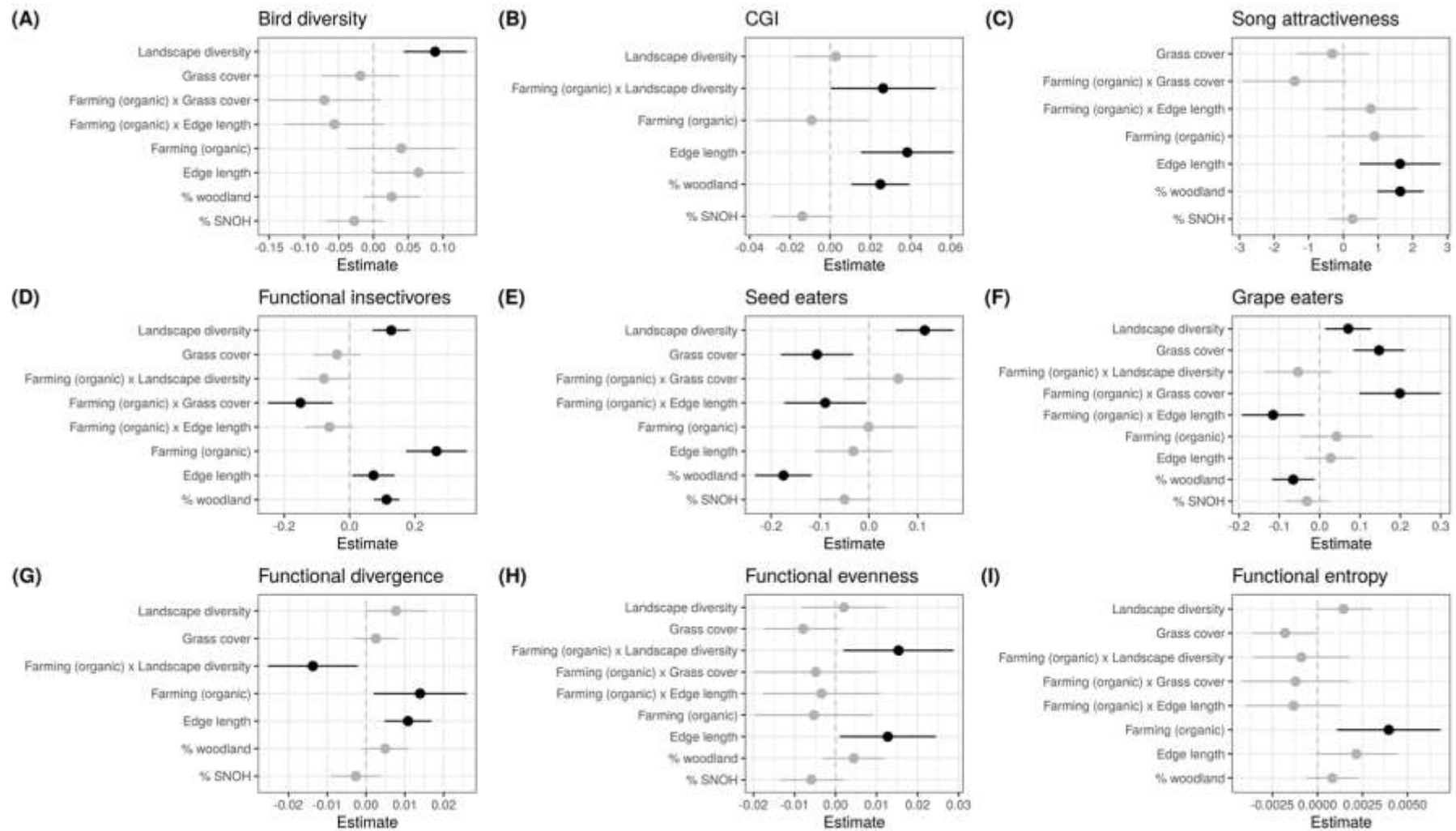


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545 Figure 1. Location map of sampled wine production regions. Clockwise from top: Bourgogne (3
546 subregions), Trentino, Lombardy (Oltrepo), Costières de Nîmes, Terrasses du Larzac, Corbières,
547 Limoux, Gaillac, Catalunya (2 subregions), Bordeaux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

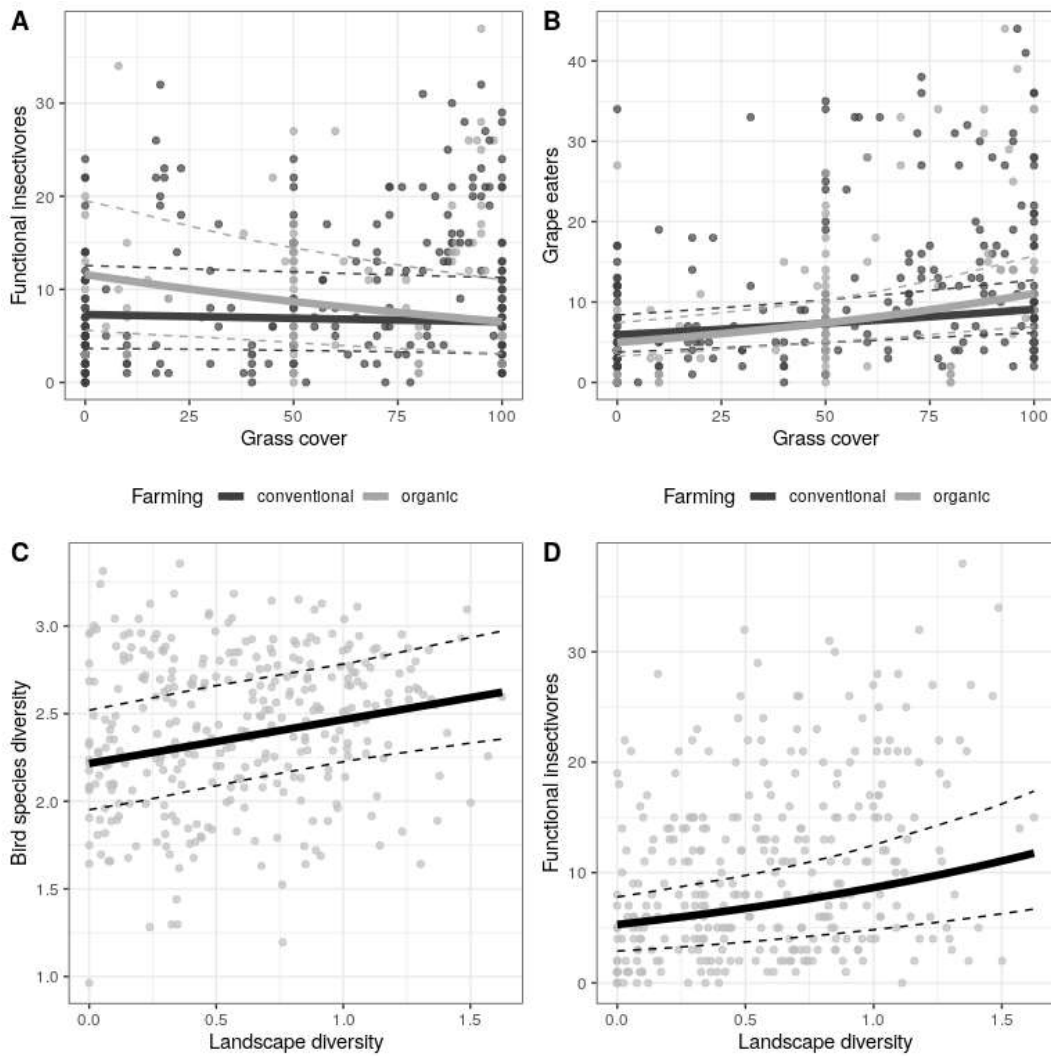


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551 Figure 2. Estimates of conditional averaged models for community metrics, avian functions and functional diversity.

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

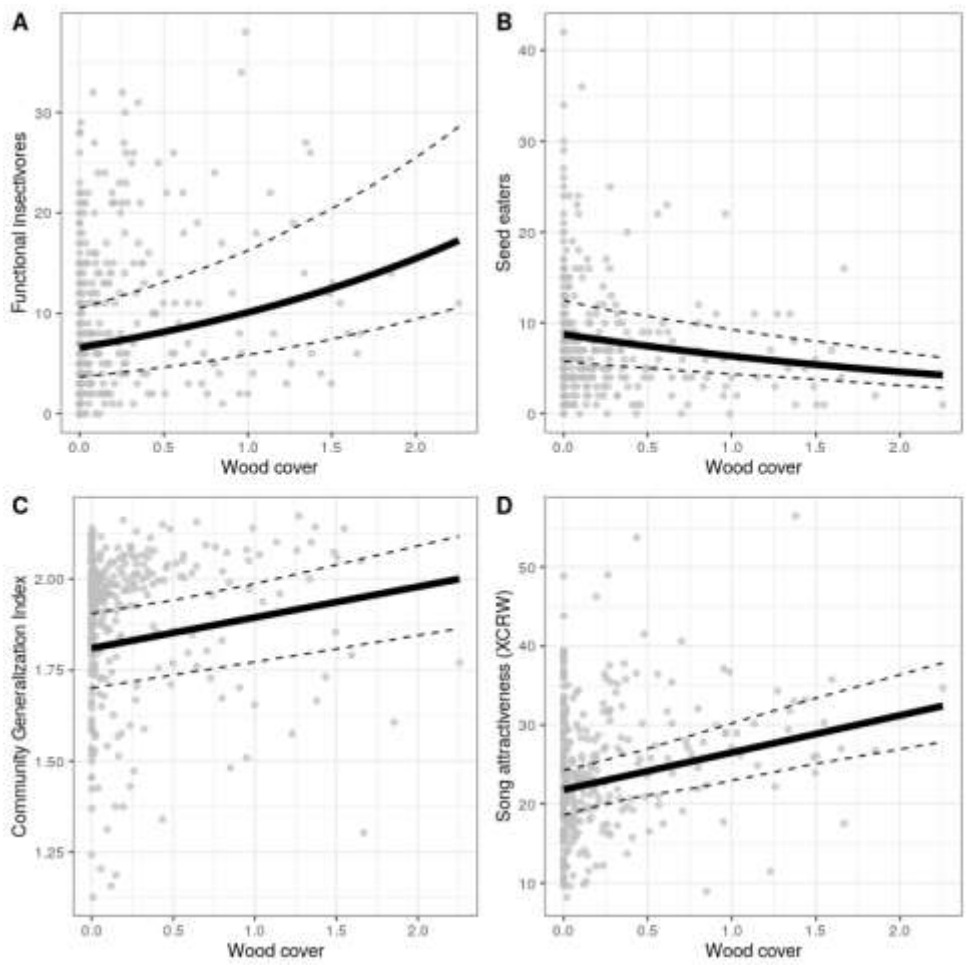
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565 Figure 4. Effects of woodland cover on bird community metrics. See Fig. 2 for estimates and
 566 confidence intervals.

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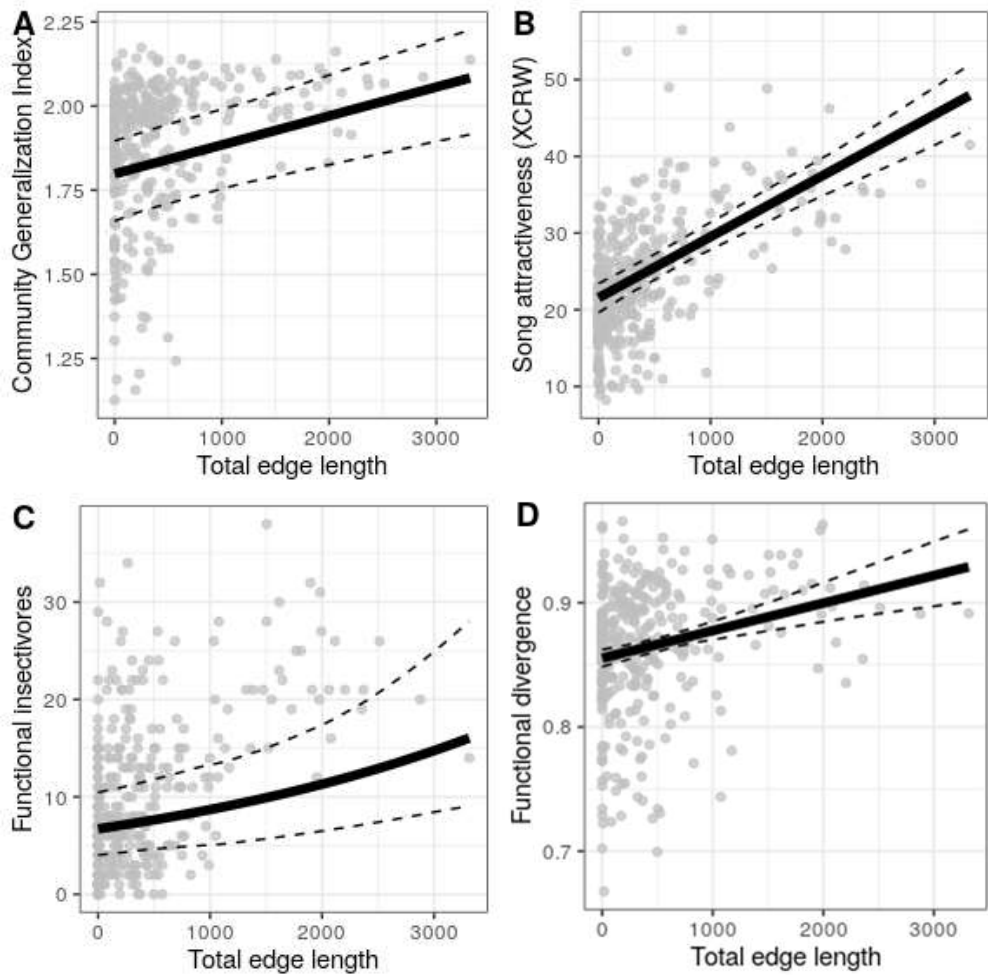


Figure 5. Effects of landscape configurational heterogeneity (edge length between vineyards and semi-natural habitats) on bird community metrics. . See Fig. 2 for estimates and confidence intervals.

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

593

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

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

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

628 The Gaillac area is located in southern France, in the Tarn district, where climate is between Oceanic
629 and Mediterranean and the altitude is low, from 105 to 288 m a.s.l. The wine growing region covers
630 8000 ha, with 2800 ha included in an AOC. Vineyards occur on sedimentary soils in the Tarn valley, in
631 the East hillsides and the Cordes plateau. The study area included 17 vineyards along a landscape
632 complexity gradient of SNH habitat cover, and about half of the stands are managed by organic
633 farming. The Limoux area is located south of Carcassonne in Aude district, at the border between
634 oceanic and Mediterranean climatic influences in southern France. The wine production area extends
635 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,
636 with two main land uses: forests (25%) and vineyards (26%).

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

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

656 In North Eastern Italy, in Trentino, the wine production area occurs between 65 m a.s.l and 750 m
657 a.s.l. and covers about 10300 ha, concentrated in the valley bottoms and their hilly sides. Vineyard
658 management is quite intensive and organic farming represented only less than 3% of the production
659 area. In addition, there are two types of vineyard structure: *pergola* is the traditional and
660 predominant one and consist in tall vines supported by a robust structure, while *spalliera* is the most
661 widespread wire arrangement. The Oltrepò Pavese area is located in the southern extreme of
662 Lombardy in the North of Italy, from the Po river (up to 50 m a.s.l) to the Apennines mountains (up to
663 1724 m a.s.l). The study was conducted on the vineyard belt (from 70 to 500 m a.s.l), which covers
664 about 15000 ha, mostly located on gently sloping hills. The area is dominated by intensively managed
665 vineyards, broadleaved woodlands and heterogeneous farming systems.

666

667

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

669

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

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673 **Appendix S3. Table of species abundance and traits**

674

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

678

679 **TBC**

680

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

683 **TBC**

684 **Functional insectivores (N = 34 species)**

685 AEGCAU
686 CISJUN
687 CLAGLA
688 CUCCAN
689 ERIRUB
690 FICHYP
691 FRICOE
692 HIPICT
693 HIPPOL
694 LUSMEG
695 MUSSTR
696 PARCAE
697 PARMAJ
698 PHOOCH
699 PHOPHO
700 PHYBON
701 PHYCOL
702 PHYLUS
703 PHYSIB
704 PRUMOD
705 REGIGN
706 REGREG
707 SAXRUB
708 SAXTOR
709 SYLATR
710 SYLBOR
711 SYLCAN
712 SYLCOM
713 SYLHOR
714 SYLMEL
715 SYLSUB
716 SYLUND
717 TROTRO
718 UPUEPO
719

720 **Seed eaters (N = 17 species)**

721 ALERUF
722 CARCAN
723 CARCAR
724 CARCHL
725 COCCOC
726 COLOEN
727 COLPAL
728 COTCOT
729 EMBCAL
730 EMBCIA
731 EMBCIR
732 EMBCIT
733 PASMOM
734 PHACOL
735 SERSER
736 STRDEC
737 STRTUR
738

739 **Grape consumers (N = 9 species)**

740 CORCOR
741 CORFRU
742 CORMON
743 GARGLA
744 PASDOM
745 STUVUL
746 TURMER
747 TURPHI
748 TURPIL
749

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

751

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

767

768