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Farmland bird assemblages exhibit higher functional and

phylogenetic diversity than forest assemblages in France

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Abstract

Aim: Under a global change scenario, research focused on changes in assembly patterns over spatial and temporal axes is more than timely as it will improve our understanding about how biological communities respond to anthropogenic disturbance. Despite an increasing need to assess whether associations among diversity and community metrics change in relation to environmental heterogeneity, the way in which community assembly rules vary across habitats has been hardly explored. Here, we tested for differences in patterns of functional diversity (FD) and phylogenetic diversity (PD) between farmland and forest bird communities.

Taxon: 107 species of breeding common birds.

Location: continental France.

Methods: We used an extensive dataset (13 years; 7,115 bird communities) from the French Breeding Bird survey in conjunction with a matrix of 142 functional traits (including information on habitat, diet, life-stories, behaviour, and morphology) to compute different metrics of FD and PD.

Results: We found that farmland assemblages showed higher FD and PD than forest assemblages, which were phylogenetically clustered. Both FD and PD of forest assemblages increased with increasing species richness, whereas in farmland assemblages the relationship turned out to be asymptotic in both cases. It may be due to the accumulation of generalists, which can end up displacing specialist species when the environment becomes oversaturated triggering a decline in diversity. Contrary to expectations, FD and PD of farmland assemblages increased over the study period, whereas forest assemblages showed a non-linear pattern. Farmland and forest assemblages also showed divergent trajectories over time in relation to FD metrics.

Main conclusions: We conclude that, although farmland intensification has led to a sharp decline in population of farmland birds, agriculture landscapes in Southern Europe still harbor diversity-rich communities probably due to the legacy effects of past land-use (traditional practices). Our study highlights the need to take into account the influence of historic landscape configurations when assessing the effect that contemporary land uses have on biotic communities.

Introduction

Community phylogenetics seeks to characterize the structure of communities and unravel the relative importance of chance (stochastic processes) and ecological rules (deterministic processes) in shaping community composition (reviewed in Pausas and Verdú 2010). Specifically, at a local scale, the quantification of functional and phylogenetic structures of assemblages allows recognition of factors leading to competitive exclusion or to the coexistence of ecologically similar taxa (environmental filtering *vs*. limiting similarity: e.g. Stevens et al. 2012). Thus, examining both biodiversity dimensions -functional and phylogenetic- turns out to be necessary for understanding the complete composition, structure and dynamics of communities (Devictor et al. 2010a).

Although several studies have assessed the phylogenetic or functional structure of bird assemblages (most of them focused on specific bird families or clades: e.g. Graham et al. 2009; Gómez et al. 2010), there is a paucity of studies examining the relationship between the phylogenetic and functional structure of assemblages and the underlying assembly processes in contrasting habitats (Thuiller et al. 2008; but see Sobral and Cianciaruso 2016; Morelli et al. 2016). This is noteworthy because it's expected that species pools and the structure of assemblages in, for example, forests and grasslands (the two extremes along a close-open continuum) are shaped by distinct ecological, evolutionary and historical mechanisms. In addition to spatial heterogeneity, the existence of temporal variability in habitat quality constitutes an important factor to consider when addressing the response of biological communities to disturbance (e.g. Méndez et al. 2012). While some habitats have undergone significant modifications during the last decades due to drastic changes in land use, some others remain unaltered and thus, they may act as true reservoirs of biodiversity. Specifically, agriculture landscapes have changed at a great pace during the last few decades due to farming intensification (Tscharntke et al. 2005). New agricultural practices have led to habitat simplification through the expansion of monocrops, the disappearance of structural elements (hedgerows, tree lines, etc.) and the abandonment of the once common practice of letting fields lie fallow. Each one of these factors seems to have contributed to the observed decline in

93   farmland bird populations (Benton et al. 2003; Donald et al. 2006). Besides species richness and

94   abundance, agricultural intensification may have an impact on other functional and structural

95   properties of biological communities. For instance, the progressive homogenization of habitat

96   structure may decrease the proportion of specialist species (Julliard et al. 2006). High Nature

97   Value (HNV) farming systems, characterized by low intensity farming and diverse, small-scale

98   mosaics of land-use types have been shown to be effective in reverting these negative effects on

99   biodiversity (e.g. Morelli 2013; Aue et al. 2014).

100   Here, we take advantage of long-term breeding bird dataset on the French avifauna to

101   investigate the processes that govern community assembly in different forest types and farmland

102   habitats managed with a different degree of intensification. Specifically, we analyze spatial and

103   temporal variation in the structure of local communities in order to address several hypotheses.

104   Firstly, in terms of phylogenetic structure, it has been argued that forests contain a greater

105   proportion of evolutionarily distinctive species compared to most human-modified habitats due

106   to its more ancient origin (Frishkoff et al. 2014). Furthermore, forests are more stable habitats,

107   favoring the colonization and successful establishment of many clades (Dreiss et al. 2015). On

108   the other hand, farmland habitats represent more unpredictable and stressful conditions, which

109   may result in physiological constraints that restrict the presence of some clades in these

110   environments (Clavel et al, 2011). Accordingly, we hypothesize that: **(1)** farmland bird

111   assemblages posse a lower phylogenetic diversity and are phylogenetically clustered, and **(2)**

112   forest bird assemblages show a pattern of phylogenetic overdispersion.

113   Secondly, it is expected that the availability and distribution of resources largely

114   determines the functional structure of communities (Weiher and Keddy 1995). Under harsh or

115   stressful conditions, environmental filtering operating on convergent traits may generate

116   functional clustering (Cavender-Bares et al. 2009), whereas in extremely productive habitats in

117   which species primarily face adversity from competition, limiting similarity may favor the

118   coexistence of species with different functional traits (Weiher et al. 1998; Gotelli et al. 2010).

119   Given that forests should provide a greater availability of niches and food resources than

120   human-modified landscapes like those resulting from agricultural practices, we predict: **(3)** a

121   stronger effect of competition in forest sites resulting in functionally overdispersed

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122   assemblages; and **(4)** a prevalence of functional clustering in farmland sites due to the higher

123   environmental harshness.

124   Thirdly, because the probability of adding new evolutionary lineages/functional groups

125   to an assemblage decreases as assemblages become more taxonomically diverse,

126   phylogenetic/functional diversity is expected to be positively associated with species richness in

127   a decelerating fashion (Cumming and Child 2009; Kluge and Kessler 2011). However, the

128   strength of this association is expected to vary depending on the evolutionary heritage of

129   communities and the evolutionary distinctiveness or 'originality' of species conforming a given

130   assemblage (Pavoine et al. 2005). As forests represent the potential natural vegetation in the

131   temperate zone and thus, they are considered older environments than more anthropic habitats,

132   we expect: **(5)** a steeper relationship (i.e. diversity level-off faster) between taxonomic and

133   phylogenetic/functional diversity in forest assemblages in comparison with farmland

134   assemblages.

135   Finally, temporal trends in diversity at the community level are expected to mirror

136   environmental changes and the anthropogenic influence on biodiversity (Magurran et al. 2010).

137   In France, farmland bird populations have fallen by one third in the last two decades (Jiguet

138   2008). Reduction in effective numbers may be accompanied by a depauperation of farming bird

139   assemblages. Meanwhile, large-scale forest maturation and afforestation have augmented in

140   most of the Southern Europe due to increased abandonment of rural land during the last century

141   and the restriction of agricultural practices to highly productive areas. Consequently, species

142   associated to forested areas seem to show a positive trend (e.g. Gil-Tena et al. 2010). Based on

143   this, we predict **(6)** the existence of differences in temporal trends between forest and farmland

144   assemblages.

145

146
147   **Material and Methods**
148   *Bird data*

149   We used abundance data on breeding birds from the French Breeding Bird Survey (*Suivi*

150   *Temporel des Oiseaux Communs*, STOC), a standardized monitoring program launched in 2001,

151   in which skilled volunteer ornithologists identify breeding birds by song or visual contact each

152   spring. Briefly, a 2×2 km plot consisting of 10-point counts -separated by at least 300 m- is

153   randomly assigned to each volunteer. Volunteers record year after year all birds seen or heard in

154   each of the ten sites during a 5-min period. Point counts are visited at dawn twice within three

155   weeks around mid-May to ensure the detection of both early- and late-breeders. The maximum

156   value of the two censuses is retained for each species as yearly abundance index. More details

157   about the scheme and census protocols are given in Monnet et al. (2014).

158   We analyzed data spanning a 13-yr period, from 2002 to 2014. Since there exist large

159   differences among the study plots in terms of sampled years, we only included those plots

160   located in farmland or forest habitats that were monitored for more than 5 years in order to

161   avoid potential biases associated to variation in sampling effort. Forest habitats comprised

162   broad-leaved, coniferous and mixed forests, whereas farmland plots were located in areas in

163   which predominates one of the following uses according to the CORINE Land Cover inventory:

164   non-irrigated arable land, complex cultivation patterns, agricultural land with significant areas

165   of natural vegetation and pastures or permanent grasslands under agricultural use. In total, we

166   gathered records from a total of 812 sites, of which 279 were located in forest habitats and 533

167   in agricultural land. Species with a large home range (raptors) and species that only breed in

168   wetlands were excluded from the analysis because they are not properly monitored by the

169   program. We also excluded species that were rarely observed and whose presence cannot be

170   considered regular, but anecdotal (i.e. rare species). Our final data set included 107 species,

171   which account for 99% of the total number of counted individuals (excluding raptors and water

172   birds).

173
174   *Functional traits*

175   A matrix of 142 traits was compiled for the 107 bird species using an extended version of the

176   dataset described in Thuiller et al. (2014). This extensive dataset includes information on

177   habitat, diet, life-stories, behaviour, morphology and reproduction providing a comprehensive

178   characterization of the ecology of each species and how they interact with the environment and

179   with other organisms (Table S1). Traits were divided into seven categories, which included both

180 multi-trait and single-trait variables. Although we used the whole set of variables to quantify

181 functional diversity (hereafter 'generic functional diversity') we also computed functional

182 diversity indices separately for habitat and feeding traits (see more below). We paid special

183 attention to these two subsets because they clearly asses different aspects of the niche, which

184 defines the level of specialization of a given species (Devictor et al. 2010b). Habitat traits reflect

185 the environmental requirements of each species and thus, the extent to which species overlap in

186 their use of space (Grinnellian or scenopoetic niche). Feeding traits reflect the trophic position

187 and the guild to which each species belongs to. That is, its place in the biotic environment and

188 the way in which each species interacts with food and other species (Eltonian or bionomic

189 niche). These groups of traits correspond to different dimensions of the niche and thus, do not

190 necessarily should exhibit congruent patterns over space or time (Cisneros et al. 2015).

191

192 *Phylogenetic and functional diversity indices*

193 *(a) Phylogenetic diversity*

194 Phylogenetic diversity (PD) reflects the accumulated evolutionary history of an assemblage, and

195 is based on the evolutionary (patristic) distance between tips in a phylogenetic tree (Faith 1992).

196 To determine overall PD, we computed the Faith's PD index (Faith 1992) and associated

197 standardized effect sizes (SES) for each of the 7,115 analyzed assemblages. This index assesses

198 species relatedness using the sum of branch lengths of the tree connecting all taxa within an

199 assemblage. Ultrametric phylogenetic distances between the 107 species were retrieved from a

200 Maximum Clade Credibility tree obtained from a sample of 100 dated, calibrated molecular

201 phylogenetic trees assembled by Thuiller et al. (2011). To assess differences that may exist in

202 phylogenetic structure between habitat types, we also computed the SES values of the mean

203 pairwise phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD),

204 respectively using the independent swap algorithm (Gotelli 2000). MNTD and Faith's PD are

205 considered "terminal" indices as they are a more sensitive to patterns occurring at the tips of the

206 tree, whereas MPD is more strongly influenced by the basal structure of the phylogenetic tree

207 (i.e. deeper branches) (Mazel et al. 2016). Negative $SES_{MPD/MNTD}$ values indicate phylogenetic

208 clustering where coexisting taxa are more related to each other than expected by chance.

209   Negative values indicate an overdispersed phylogeny where coexisting taxa are less related to

210   each other than would be expected at random. SES_{PD}, SES_{MPD} and SES_{MNTD} values were

211   calculated using the R package *picante* (Kembel et al. 2010).

212

213   *(b) Functional diversity*

214   Functional diversity (FD) represents variability in ecological traits among species, reflecting the

215   'ecological robustness' or resilience of assemblages, which is relevant in order to assess the

216   capacity of an ecosystem to respond effectively to global change (Villéger et al. 2008). As an

217   overall measure of FD, we used the Rao quadratic entropy index (Botta-Dukát 2005), a

218   generalization of the Simpson's index of biodiversity. Rao's index represents the average

219   dissimilarity between all co-occurring species in the same assemblage and is greater as the

220   number of functionally unique species increases (Laliberté and Legendre 2010). We calculated

221   the standardized effect size of Rao (SES_{Rao}) using the 'melodic' function (de Bello et al. 2016).

222   SES_{Rao} quantifies the number of standard deviations (SD) that observed Rao values are above or

223   below the mean Rao of random assemblages and it has proven an accurate metric of FD (Mason

224   et al. 2013; Mouchet et al. 2010). Under the null hypothesis of random trait distribution in

225   species assemblages, mean SES_{Rao} equals zero. As a result, SES_{Rao} negative values indicate trait

226   convergence (i.e. assemblages formed by taxa sharing more similar traits than expected by

227   chance), while positive values indicate trait divergence (i.e. assemblages formed by taxa with

228   more distinct traits than expected at random). We tested whether annual values of FD were on

229   average significantly different from values expected at random by means of Student's *t*-tests,

230   comparing observed SES_{Rao} values with the null hypothesis ($\mu = 0$) (Kembel et al. 2010). In

231   addition, we obtained a functional dendrogram to compute tree-like FD indices (mean

232   functional distance, MFD, and mean nearest taxon distance, MNTD) and associated SES values

233   (SES_{MFD} and SES_{MNTD}) in an analogous way to that previously reported.

234   We also computed three complementary multidimensional FD metrics: functional

235   richness (FRic), functional divergence (FDiv) and functional evenness (FEve) (Mason et al.

236   2005; Villéger et al. 2008). An interpretation of these metrics is provided in Table 1. As the trait

237   matrix included binary and continuous trait variables, we previously performed the following

8

238   steps in order to obtain a new set of 'traits' suitable to be used as input when computing the FD

239   indices. First, a generalization of Gower's distance was employed to calculate multivariate

240   distances between species based on the raw trait data (Pavoine et al. 2009). We made sure the

241   seven trait categories had a similar weight using the 'dis.ktab' function in the R package *ade4*

242   (Dray and Dufour 2007). The resultant species × species dissimilarity matrix was then subject to

243   a Principal Coordinates Analysis (PCoA) and the six first axes of this ordination were used to

244   build a six-dimensional convex hull from which we computed FRic, FDiv and FEve using the

245   function 'multidimFD' developed by Sebastien Villéger. We computed these three metrics from

246   the complete matrix of 142 traits as well as separately for Grinnellian and Eltonian traits using a

247   matrix of habitat and feeding dissimilarity respectively. We used generalized linear mixed

248   models (Pinheiro and Bates 2009), in which FRic/FDiv/FEve was considered the response

249   variable and habitat type the explanatory variable to test for differences between forest and

250   farmland assemblages. Models included study year, taxonomic richness, and study plot (to

251   account for variability in the level of indices among sites) as covariates and random effect,

252   respectively.

253

254   *Relationship between species richness and structure of assemblages*

255   In order to explore the relationships between species richness (SR) and the phylogenetic and

256   functional structure of assemblages, we correlated mean values (averaged over years) of species

257   richness, SES_{PD} and SES_{Rao} for each of the 812 study plots by means of Pearson's correlations.

258   We obtained similar results when considering each community as an independent sampling

259   point (i.e. one point per community; $n = 7,115$ communities) (analyses not shown).

260

261   *Temporal trends in phylogenetic and functional diversity*

262   We modeled bird diversity trends over the 2002-2014 timeframe to test whether forest and

263   farmland assemblages exhibit similar temporal patterns. We considered five response variables:

264   SES_{PD}, SES_{Rao}, FRic, FDiv and FEve. All these response variables were scaled to null mean and

265   unit standard deviation (z-scores) prior to modeling in order to facilitate direct comparisons

266   among them. We used generalized additive mixed models (GAMM) (Wood 2006) in which

267   trends were quantified by a continuous penalized spline with a degree of smoothness estimated

268   by generalized cross validation (constrained to a maximum of 4 to avoid unjustified

269   complexity). We included study plot as random effect to account for variability in the level of

270   indices among sites and controlled residual spatial autocorrelation with an unconstrained two-

271   dimensional (latitude, longitude) spline. We further added taxonomic richness as a spline

272   covariate in all models with FRic, FDiv or FEve as response variable to correct statistically the

273   sampling-mediated positive relationship between the number of species and the trait range in an

274   assemblage (Barnagaud et al. 2017).

275

276

277   **Results**

278

279   *Differences in phylogenetic and functional structure between farmland and forest communities*

280   Although farmland and forest assemblages harbor a quite similar number of breeding common

281   species (mean ± SE; *farmland*: 34.54 ± 7.00, range: 11-56; *forest*: 32.97 ± 7.25, range: 10-56),

282   farmland communities show a considerably higher phylogenetic diversity in comparison with

283   forest communities ($t = -11.07$, $p<0.001$) (Fig. 1a). Annual average values of phylogenetic

284   diversity (PD) were significantly greater than zero in farmland assemblages throughout the

285   study period, which suggests a prevalence of phylogenetic overdispersion in these communities

286   (Fig. 2). Instead, all annual averages for forest assemblages were negative indicating a trend

287   towards phylogenetic clustering (Fig. 2). Accordingly, standardized effect sizes of mean

288   pairwise phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) values were

289   lower in forest assemblages in comparison with farmland assemblages (SES_{MPD}, *forest*: -0.49 ±

290   0.71, *farmland*: 0.10 ± 0.38; SES_{MNTD}, *forest*: -0.53 ± 0.75, *farmland*: -0.22 ± 0.71; Fig. 1a)

291   (both p-values <0.001). In farmland communities, SES_{PD} values increased over the study period,

292   while these showed a 'hump-shaped' pattern in forest assemblages (Fig. 3a).

293   In terms of functional diversity (FD), although mean SES_{Rao} values were negative in

294   almost all cases (Fig. 2), forest assemblages showed significantly lower values in comparison

295   with farmland assemblages (*forest*: -0.48 ± 0.40, *farmland*: -0.04 ± 0.33; $t = -19.26$, $p < 0.001$).

296 In both habitats, temporal trends for SES_{Rao} values followed a similar pattern to that observed

297 for PD (Fig. 3a), indicating a tight correlation between both facets (farmland: $\rho = 0.27$, p

298 <0.001; forest: $\rho = 0.51$, p<0.001). The obtained values for both metrics of functional structure

299 (SES_{MFD} and SES_{MNTD}) indicated that forest assemblages exhibit a stronger signature of

300 functional clustering (SES_{MFD}, *forest*: -0.39 ± 0.35, *farmland*: -0.11 ± 0.72; SES_{MNTD}, *forest*: -

301 0.33 ± 0.39, *farmland*: -0.20 ± 0.70; Fig. 1a) (both p-values <0.001).

302   Farmland communities also differed significantly from those in forests with respect to

303 two of the three complementary functional diversity indices; functional richness (FRic) and

304 divergence (FDiv) (Table 1). Overall, farmland communities occupy a greater amount of

305 functional space than forest assemblages irrespective of the category to which they belong to

306 (Fig. 4). Temporal trends in FRic and FDiv for farmland and forest assemblages showed

307 divergent patterns (Fig. 3b). Trait range (FRic) and spread (FDiv) within the functional space

308 decreased in the forest assemblages, whereas both indices tended to increase in farmland

309 communities. Bird assemblages appeared to become less functionally even over the study period

310 (Fig. 3b).

311   When grouping functional traits into different categories (subsets), we observed that,

312 similar to generic FD, the FRic and FDiv of both feeding and habitat traits were greater in

313 farmland assemblages (Table 1). In contrast, the regularity of species' abundance distribution in

314 the functional space (functional evenness) did not differ significantly between farmland and

315 forest assemblages in either case (Table 1). It means that, although the amount of niche space

316 filled tend to vary between farmland and forest assemblages, the way in which this space is

317 filled does not differ between habitats.

318

319 *Species richness* versus *structure of assemblages*

320 The sign of the relationship between species richness (SR) and both functional and phylogenetic

321 structure varied between habitat categories. Both PD and FD of forest assemblages increased

322 with increasing SR, indicating that poor assemblages were phylogenetic and functionally

323 clustered and that random patterns have a greater influence in richer assemblages (PD: $\rho = 0.37$,

324 p <0.001; FD: $\rho = 0.38$, p<0.001; Fig. 5, Fig. S1). In contrast, in farmland assemblages, the

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325 correlation between SR and phylogenetic and functional structure was non-significant in either

326 case (both p-values > 0.1). Rather, the relationship turned out to be asymptotic in both cases

327 (Fig. 5, Fig. S1). In fact, albeit non-significant, the model that included the quadratic term of SR

328 provided a better fit to the data than did the model including the linear term of SR (PD, *SR*:

329 estimate = 0.37 ± 0.27, t = 1.35, p = 0.17; *SR*^{2}: estimate = -0.79 ± 0.27, t = -2.88, p <0.01; FD,

330 *SR*: estimate = 0.06 ± 0.26, t = 0.23, p = 0.81; *SR*^{2}: estimate = -0.43 ± 0.26, t = -1.66, p = 0.09).

331

332

333 **Discussion**

334 *Phylogenetic structure*

335 Although it is expected that severe habitats such as savannas (Almeida et al. 2018) and

336 agricultural landscapes (Deikumah et al. 2017) tend to harbor assemblages with lower

337 phylogenetic diversity (PD) because the persistence of some lineages is jeopardized, we found

338 the opposite pattern; forest assemblages exhibited lower PD than those located in farmlands.

339 This result indicates that, although farmland intensification has led to a sharp decline in

340 populations of farmland birds, agriculture landscapes still harbor phylogenetically rich

341 communities probably due to the legacy effects of past land-use (Farina 1997). The

342 Mediterranean basin has experienced thousands of years of human landscape modification for

343 livestock and agricultural purposes, with forest destruction the most obvious consequence of

344 such an action (Blondel 2006). As a result of traditional landscape design and management by

345 humans, and in discordance with general assumptions on the relationship between biodiversity

346 and habitat degradation, Mediterranean bird communities do not reach their maximum

347 biodiversity in pristine oak woodland, but in agro-sylvo-pastoral landscape mosaics (Blondel

348 and Aronson 1999). In addition, it has been suggested that most of the few bird groups that

349 differentiated within the Mediterranean region are fundamentally birds of open habitats and

350 scrublands (e.g. *Sylvia* species) (Covas and Blondel 1998). All these factors may have

351 contributed to the existence of a higher diversity in farmland assemblages. In this respect, it

352 should be noted that the Mediterranean region only comprises a relatively small portion of

353   continental France. However, traditional agroforestry systems in other French regions share key

354   features with those typical from Mediterranean environments *sensu stricto*. For example,

355   original *bocages*, prevalent in Western France (Atlantic zone), consist of permanent meadows

356   used for livestock farming divided into small hedged fields interspersed with groves of trees,

357   which provide shelter and food for a host of animals. This patchwork-like environment dating

358   back from the Iron Age is evolving rapidly in a trend towards simplification (Pointereau and

359   Bazile 1995). Thus, intermediate levels of human-induced disturbance throughout civilizations

360   seem to have contributed to keeping rural landscapes heterogeneous and promoting biological

361   diversity. At the present time, agricultural communities may still bear the imprint of historical

362   landscape configurations, which is thought to persist for decades or centuries due to the lagged

363   response of species to landscape change ("ghosts of landscape past"; With 2007).

364   On the other hand, most forests in the temperate zone -including Southern Europe- are

365   secondary forests that developed after logging of primeval forests or abandonment of

366   agricultural lands (Blondel 2018). Species inhabiting these forests constitute an impoverished

367   subset of the pool of forest specialists from the Nearctic-Palearctic region, many of them being

368   habitat generalists able to colonize a wide variety of forest environments (Covas and Blondel

369   1998). Hence, Southern Europe forests would have lost most of the forest specialists a long time

370   ago. In fact, we found that forest communities are made up of species with a lower degree of

371   specialization than those conforming farmland assemblages (Gini specialization index; *forest*:

372   0.20 ± 0.03, *farmland*: 0.22 ± 0.03; see Fig. S2). Such a circumstance, coupled with habitat

373   fragmentation, could explain the existence of strong phylogenetic underdispersion in forest

374   communities. On the contrary, the level of clustering was much lower in farmland assemblages,

375   mostly in plots with significant areas of natural vegetation. It suggests that the presence of

376   structural elements such as field margins, hedgerows and non-cultivated areas (small woodland

377   patches) increases substantially the diversity of lineages that colonizes and persists in these

378   environments (e.g. Doxa et al. 2012). The existence of a subtler signature of environmental

379   filtering may have to do with the fact that domestications of animals and plants began about

380   4,000 years ago in this region and agriculture environments had been occupied repeatedly by

381 phylogenetically-divergent lineages in multiple colonization events along its long and dynamic

382 history (Blondel 2006).

383

384 *Functional structure*

385 In terms of functional diversity (FD), and in accordance with the phylogenetic results, we found

386 a higher FD in farmland assemblages. A similar result has been previously observed in northern

387 Spain (Clavero and Brotons 2010), central Italy (Morelli et al. 2018) and tropical montane

388 Ethiopia (Gove et al. 2013), which indicates that bird communities in certain agricultural

389 landscapes sustain distinct species from an ecological perspective. Whilst, in concert with that

390 reported in terms of phylogenetic structure, forest assemblages showed a higher degree of

391 functional clustering, which means that they harbor a greater number of functionally similar

392 species.

393   The highest values of functional richness (FRic) were found in communities from low-

394 intensity farmlands (agricultural land with significant proportions of natural vegetation), which

395 represent traditional land uses. At the opposite end, coniferous forests constitute the habitat type

396 supporting the lowest values of FRic probably due to its low spatial heterogeneity in vertical

397 and horizontal structure (Fig. 4). Differences in FRic between farmland and forest assemblages

398 were less pronounced when considering only Eltonian traits because the low richness in terms

399 of species' feeding traits observed in communities located in lands dominated by complex

400 cultivation patterns or non-irrigated land. It suggests a reduced trophic-niche space in the most

401 anthropogenized and simple agricultural landscapes.

402   Obtained values of functional divergence (FDiv) indicate a higher degree of niche

403 differentiation among species within farmland communities in comparison with forest

404 communities. That is, the most abundant species in farmland assemblages are very dissimilar

405 which may be due to -as above mentioned- limiting similarity precludes the co-existence of

406 functionally redundant taxa, or the availability of a great variety of feeding resources (open

407 fields for seed-eating species, bushes for frugivorous species and groves of trees for those that

408 are canopy-gleaners) and nesting substrates in some agricultural systems. Differences in FDiv

409 between habitats remained when analyzing Eltonian and Grinellian traits separately, which

410   implies the existence of a higher level of differentiation in farmland assemblages at different

411   dimensions of the niche.

412   Regarding the way in which the biomass of the species assemblage is distributed in

413   niche space (functional evenness, FEve), our results suggests that ecological resources are

414   exploited in a pretty similar manner in both habitats. It means that the availability of niches

415   potentially available but unused by the bird species of the community does not differ between

416   farmlands and forests, a similar result to that reported by Morelli et al. (2018). According to the

417   obtained FEve values, both habitat types exhibit a moderate uniformity of species in functional

418   space (intermediate FEve values; Fig. 4). Thus, by using functional evenness as proxy of

419   community resilience, we hypothesize that farmland and forest assemblages are equally

420   vulnerable to modifications (e.g., climate change or biological invasions).

421   In terms of functional structure, forest bird assemblages showed a pattern of clustering,

422   contradicting our initial hypothesis of functional repulsion as result of the prevalence of limiting

423   similarity in more benign habitats. This result agrees with that reported in forest bird

424   assemblages from the Cerrado (Sobral and Cianciaruso, 2016) and the Brazilian Atlantic Forest

425   (Rocha et al. 2019). Although temperate forests are not as structurally complex and dense as

426   rainforests from the tropical region, one possibility is that closed habitats (i.e. forests) act as

427   local environmental filter restricting the occurrence of large birds or those that require open

428   country (e.g. ground-feeding insectivores like pipits and larks).

429

430   *Relationship between taxonomic richness and structure of assemblages*

431   The shape of the relationships between metrics of biodiversity and taxonomic richness differed

432   between habitats. While in forest habitats, PD and FD increased linearly with increasing species

433   richness with no evidence of a saturating effect, within farmlands such a relationship seems to

434   be asymptotical indicating that beyond a certain threshold (~35 spp.) both dimensions of

435   biodiversity tend to decay (Fig. 5) (see also Hanspach et al. 2015). It suggests that forests are

436   less-redundant systems than farmlands, in which an increase in the number of species not

437   necessarily increase the functional diversity of the community. Such a pattern may be due to the

438   accumulation of generalist species, which can end up displacing specialist species when the

439 environment becomes oversaturated triggering a decline in diversity (Clavero and Brotons

440 2010).

441

442 *Temporal trends*

443 Phylogenetic and functional diversity of farmland bird assemblages increased over the period

444 indicating that decreasing bird abundances in agricultural landscapes are not associated with a

445 phylogenetic impoverishment or functional homogenization of local bird assemblages. This

446 tendency was not observed in forest assemblages, where diversity trends showed a non-linear

447 pattern. In a similar way, multidimensional FD indices presented distinct temporal trends in

448 both habitat types. Whereas the volume of functional space and the distribution of species

449 within the convex hull have decreased over time in forest assemblages, these metrics tend to

450 show a positive trajectory in farmland communities. It indicates that the drastic declines

451 documented in bird populations across the French countryside have not led to a depaupuration

452 of local communities in terms of PD and FD. This finding could be due to the existence of a

453 time-lag or a decoupling between the mechanisms regulating species populations (e.g. niche

454 processes) and community-level properties that emerge from these species, which heavily

455 depend on biotic interactions. Hence, compensatory dynamics could explain the existence of a

456 decrease in functional richness of forest communities despite most forest species show stable

457 trends if, for example, increases in the populations of forest species are offset by decreases in

458 the populations of transient species (Santini et al. 2017). In this sense, species populations and

459 diversity indices could exhibit different responses to disturbances, which highlights the need for

460 a better understanding of how the impacts of shifts at the species level relate to community-level

461 descriptors (Supp and Ernest 2014).

462   Lastly, a caveat of this study is that we did not account for imperfect detection of

463 species in our analyses, a factor that may depend on the habitat type in which the survey is

464 conducted. For instance, in a recent study, Kułaga and Budka (2019) compared the number of

465 bird species detected through human observers (in the field) and recordings by autonomous

466 sound recorders (manually analyzed by observers in the lab) within two different habitats -forest

467 and farmland- in Poland. They reported that observers detected more species than recorders in

16

468   farmland, but not in the forest (Kułaga and Budka, 2019). Regarding this, we have to point out

469   that although our results should be interpreted with caution, this potential bias does not affect

470   the main findings of this study, that is, the different trajectory that farmland and forest

471   assemblages exhibit over time.

472

473   *Conclusions*

474   Several intriguing ideas for both community ecologists and conservationists arise from this

475   study considering that agro-ecosystems constitute one of the most common landscapes

476   throughout the world and represent the main habitat for many bird species (Pain and Pienkowski

477   1997). First, our study supports the notion that heterogeneous landscapes in which

478   environmental conditions change significantly within short distances resulting in small-scale

479   mosaics typical of the Mediterranean Basin and Western France, may benefit generalist species

480   and impose limits to the potential ranges of species requiring large continuous areas of forest.

481   Second, phylogenetic diversity can be a surrogate for high-dimensional trait diversity and thus,

482   by protecting more phylogenetic diversity, we should also protect a greater amount of total

483   functional diversity (Faith 2018). Third, some of the observed patterns suggest that past land use

484   may generate strong legacy effects on biotic communities and thus, it's necessary to consider

485   the influence of historic landscape configurations when assessing the effect that contemporary

486   configurations have on them. Finally, and regarding this latter, community-level properties may

487   be particularly resilient to land use alterations and thus, their accuracy as indicators of change

488   may be limited. Consequently, gaining a better understanding of how changes at the species

489   population level scale up to shape community properties constitutes a major challenge for

490   biodiversity research.

491

500

501 *Data accessibility*: The dataset employed in this study will be deposited in a public repository

502 upon acceptance.

503 *Conflict of interest*: The authors declare that they have no conflict of interest.

504
505 *Biosketch*

506 **Vicente García-Navas** is a FCT researcher at the University of Lisbon. His work addresses

507 how historical, phylogenetic and spatial patterns of eco-morphological and lineage diversity are

508 influenced by biotic and abiotic factors and the interaction between them.

509

510 **Wilfred Thuiller** is a senior scientist at CNRS based in Grenoble. His research is focused in

511 investigating the impacts of global change on biodiversity.

512

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698 **Table 1.** Descriptive summary (means ± SE) of habitat differences in French bird functional diversities for the 2002-2014 period. Functional richness (FRic) is

699 the amount of the functional space filled by the community; functional divergence (FDiv) measures the degree to which the abundance of a community is

700 distributed toward the outer margins of occupied trait space and can thought of as functional 'specialization'; functional evenness (FEve) quantifies the

701 regularity of species' abundance distribution in the functional space to allow effective utilization of the entire range of resources available.

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Indices	Farmland ($n = 4{,}749$)	Forest ($n = 2{,}366$)	test (p-value)
Generic functional diversity (142 traits)			
FRic	0.243 ± 0.098	0.172 ± 0.110	-14.74 (<0.001)
FDiv	0.858 ± 0.034	0.831 ± 0.036	-12.41 (<0.001)
FEve	0.667 ± 0.054	0.664 ± 0.056	-0.77 (0.44)
Habitat – *Grinellian niche* (81 traits)			
FRic	0.163 ± 0.098	0.134 ± 0.108	-3.10 (<0.01)
FDiv	0.843 ± 0.049	0.795 ± 0.049	14.88 (<0.001)
FEve	0.543 ± 0.056	0.541 ± 0.057	-0.66 (0.51)
Feeding – *Eltonian niche* (38 traits)			
FRic	0.229 ± 0.108	0.225 ± 0.113	3.57 (<0.001)
FDiv	0.840 ± 0.033	0.822 ± 0.033	-9.97 (<0.001)
FEve	0.613 ± 0.055	0.619 ± 0.057	1.71 (0.08)

Figure captions

707

708 **Figure 1.** Differences in phylogenetic diversity (PD) and phylogenetic structure (left), and

709 functional diversity (FD) and functional structure (right) among breeding bird assemblages from

710 farmlands and forests. Bars are equivalent to confidence intervals of 95%. The two main habitat

711 types are broken down into different habitat categories according to the CORINE Land Use

712 classification (1: agricultural land with significant areas of natural vegetation, $n = 260$; 2:

713 pastures or permanent grasslands under agricultural use, $n = 1397$; 3: non-irrigated arable land,

714 $n = 2112$; 4: complex cultivation patterns, $n = 980$, 5: mixed forest, $n = 321$; 6: broad-leaved

715 forest, $n = 1559$; 7: coniferous forest, $n = 486$). SES_{PD} = standardized effect sizes of PD;

716 $SES_{MPD/MFD}$ = standardized effect sizes of MPD/MFD; SES_{MNTD} = standardized effect sizes of

717 MNTD (computed from both phylogenetic and functional distances). Habitat differences

718 remained statistically significant when using raw values of PD (farmland: 1709 ± 277; forest:

719 1586 ± 304).

720

721 **Figure 2.** Annual mean values ($\pm 95\%$ CI) of phylogenetic (SES_{PD}) and functional diversity

722 (SES_{Rao}) and results of *t*-tests testing whether values were significantly different from zero (*p*-

723 values in brackets; ***: <0.001; **: <0.01; *: <0.05; *ns*: >0.05). Negative standardized metric

724 reflects a relative clustering of species while a positive standardized metric reflects a relative

725 overdispersion of species.

726

727 **Figure 3.** Temporal trends in (a) phylogenetic (SES_{PD}) and generic functional (SES_{Rao})

728 diversity, and (b) multidimensional functional diversity metrics (FRic, FDiv and FEve) over the

729 study period (2002-2014). Trends are represented as smoothed curves fitted with GAMM.

730 Diversity indices were scaled to mean $= 0$ and SD $= 1$ to ease comparisons.

731

732 **Figure 4.** Functional diversity quantified in terms of functional richness, functional divergence,

733 and functional evenness of farmland and forest bird assemblages in France over the period

734 2002-2014. Values were standardized as *z*-cores to facilitate comparison among the different

735   subsets. Bars represent 95% confidence intervals. The two main habitat types are broken down

736   into different habitat categories according to the CORINE Land Use classification for illustrative

737   purposes (see Fig. 1). Pictures describing each habitat category were obtained from the

738   Copernicus website (https://land.copernicus.eu/).

739

740   **Figure 5.** Relationship between species richness of forest and farmland bird assemblages and

741   their respective standardized effect size (SES) of phylogenetic (Faith's PD) and functional (Rao

742   index) diversity. Overplotting (density) of points is indicated by darker shades of gray. In the

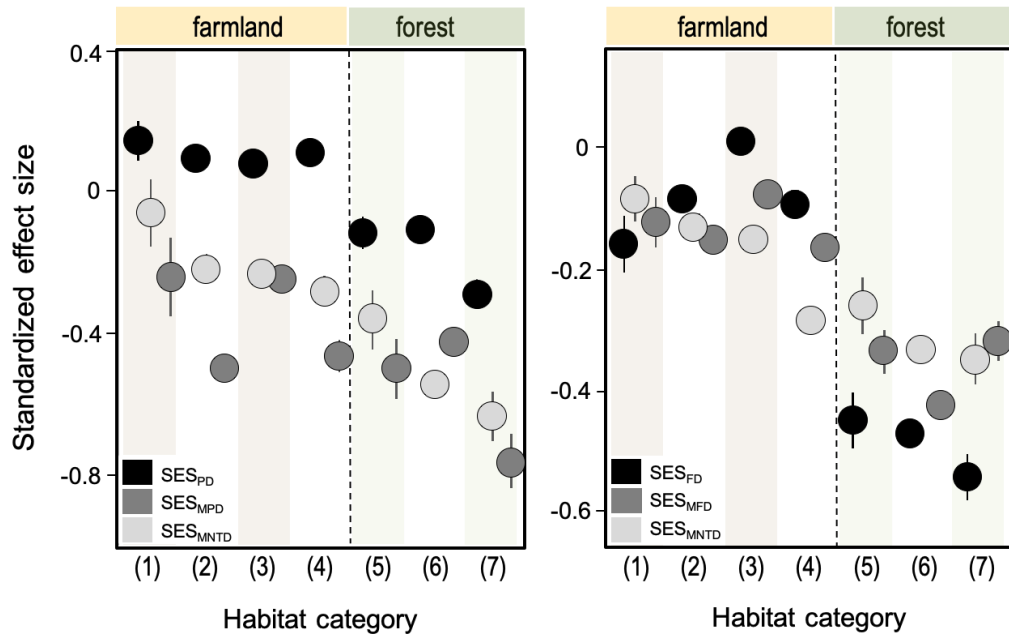743   insets, polynomial functions were fitted to visualize trends in the data.
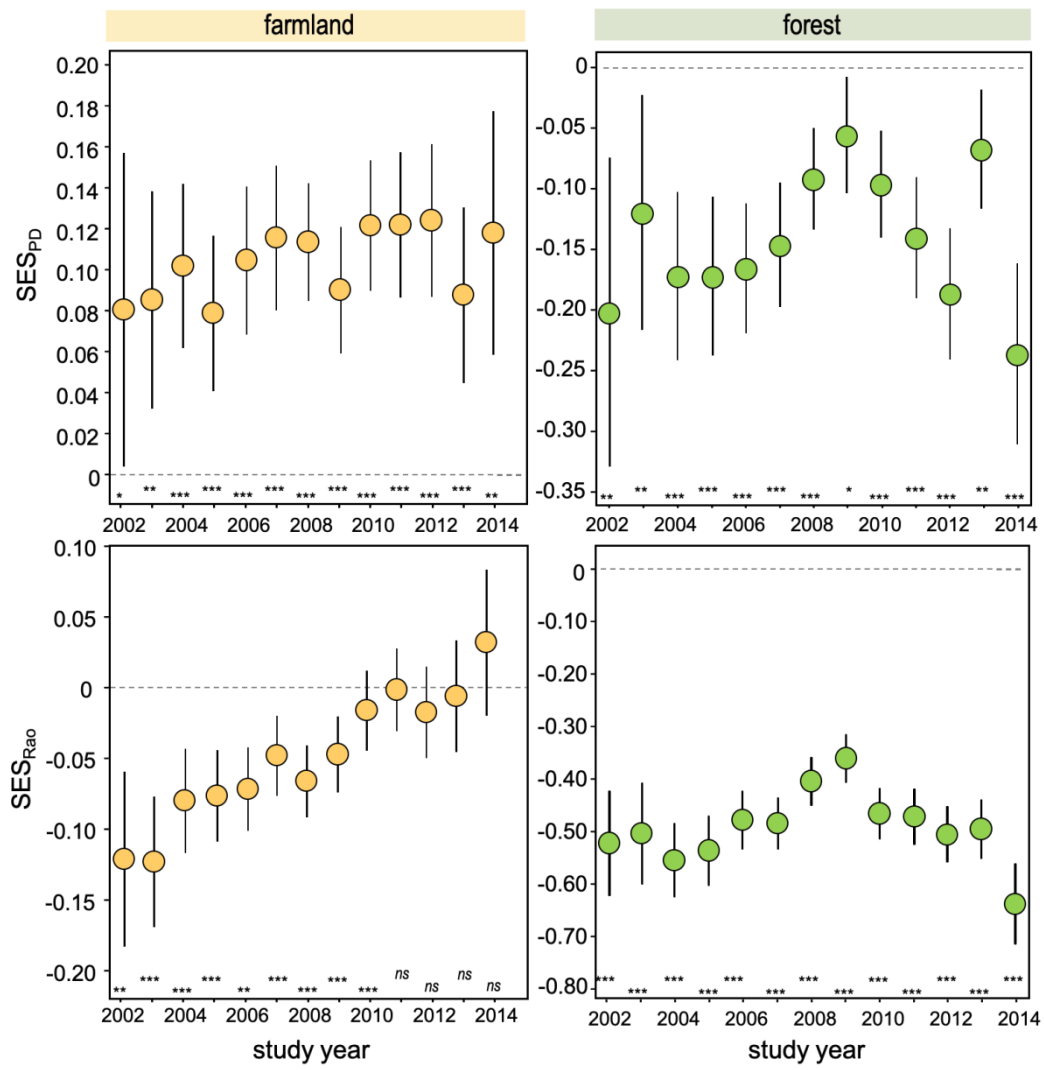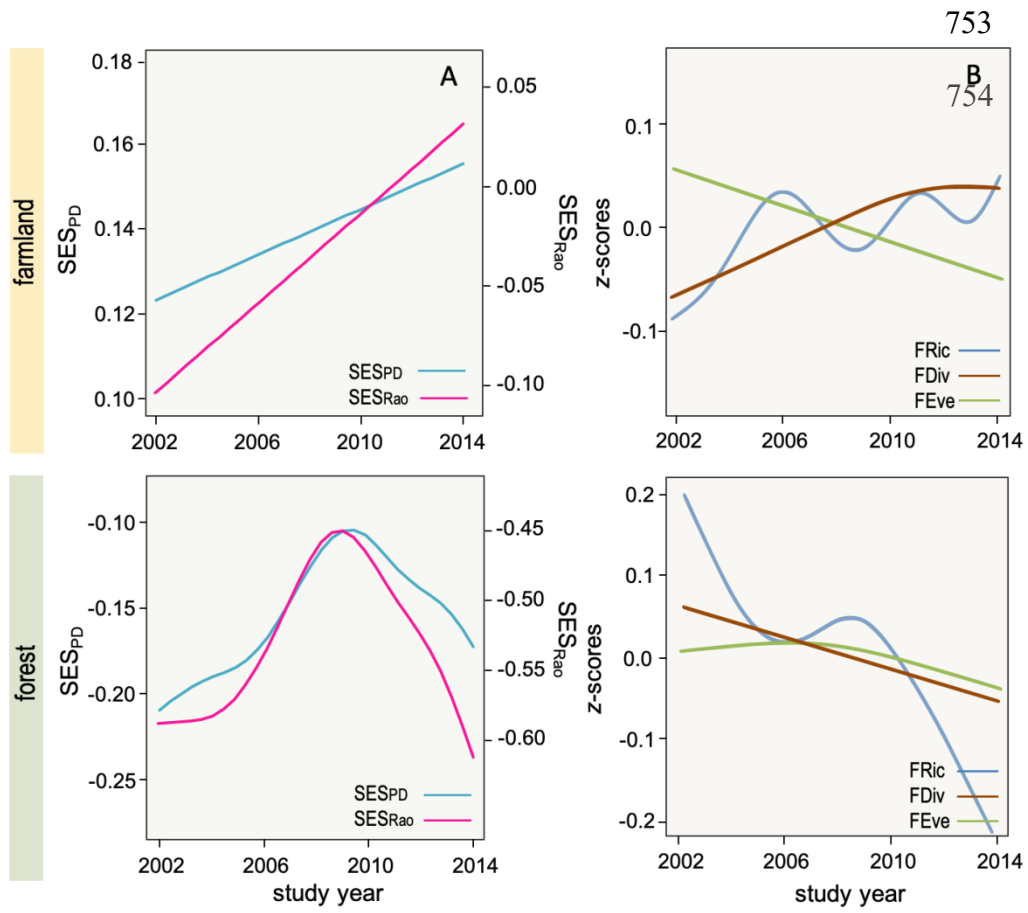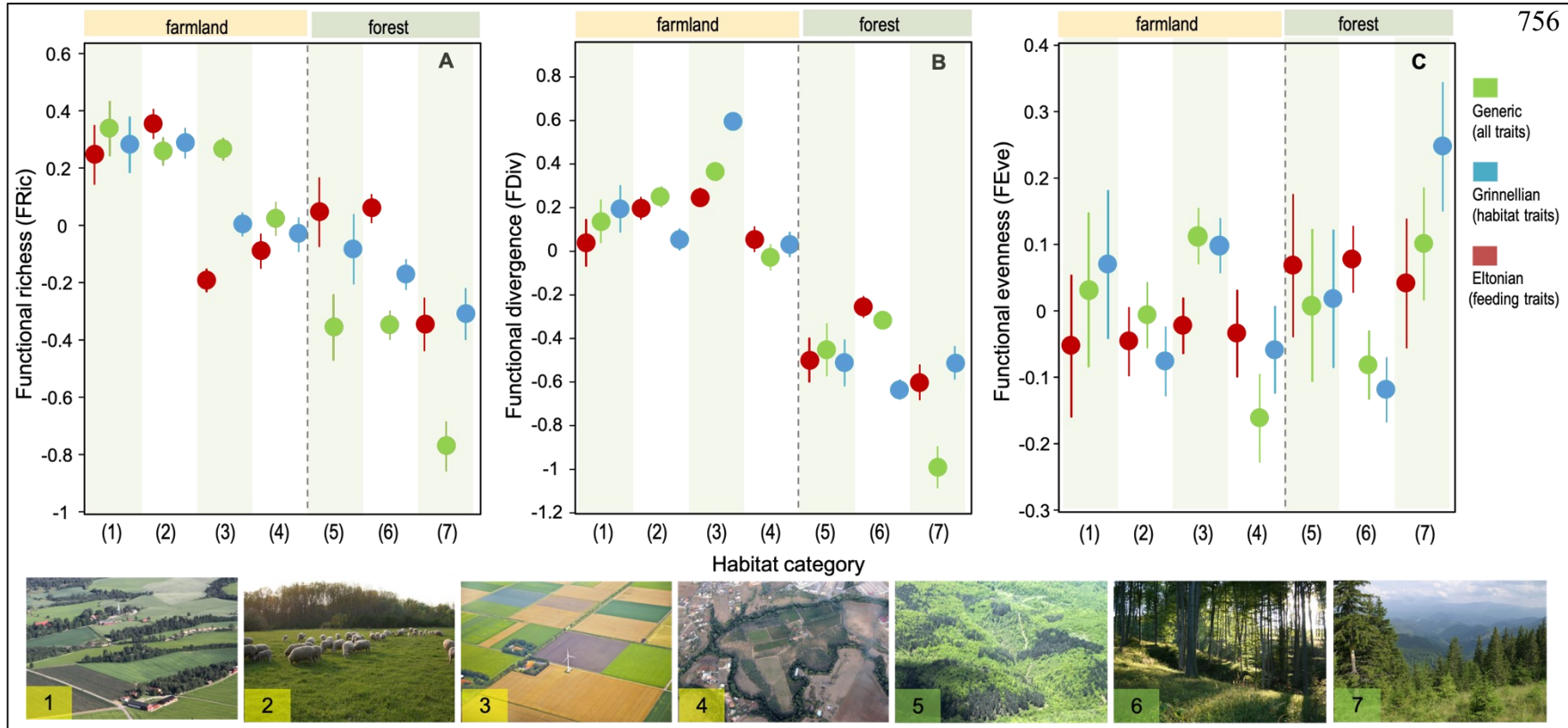
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746   Figure 1

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Figure 4

Figure 5

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