RESEARCH PAPER

Farmland bird assemblages exhibit higher functional and phylogenetic diversity than forest assemblages in France

Vicente García-Navas[1,2,3] | Wilfried Thuiller[1]

[1]Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Ecologie Alpine, F-38000, Grenoble

[2]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[3]Department of Evolutionary Genetics, Centre for Ecology, Evolution and Environmental Changes (CE3C), University of Lisbon, Lisbon, Portugal

Correspondence
Vicente García-Navas, Department of Evolutionary Genetics, Faculdade de Ciências da Universidade de Lisboa, Edifício C2, 5º Piso, Campo Grande, 1749-016 Lisboa, Portugal.
Email: vicente.garcianavas@gmail.com

Abstract

Aim: Under a global change scenario, research focused on changes in assembly patterns over spatial and temporal axes is paramount. 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 in order to improve our understanding about how biological communities respond to anthropogenic disturbances.

Location: Continental France.

Taxon: 107 species of common birds.

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 and examine how these vary between habitat types and across time.

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 was asymptotic in both cases. This pattern 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: Although farmland intensification led to a sharp decline in populations of farmland birds, agricultural landscapes in southern Europe still harbour 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 historical landscape configurations when assessing the effect that contemporary land uses have on biotic communities.

KEYWORDS
agriculture, avifauna, biodiversity, community dynamics, functional traits

1 | 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 & 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 versus limiting similarity: e.g. Stevens, Gavilanez, Tello, & Ray, 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, Mouillot, et al., 2010).

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. Gómez, Bravo, Brumfield, Tello, & Cadena, 2010; Graham, Parra, Rahbek, & McGuire, 2009), 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 & 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 may act as true reservoirs of biodiversity. Specifically, agricultural landscapes have changed at a great pace during the last few decades due to farming intensification (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 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 farmland bird populations (Benton, Vickery, & Wilson, 2003; Donald, Green, & Heath, 2001; Donald, Sanderson, Burfield, & Van Bommel, 2006). Besides species richness (SR) and abundance, agricultural intensification may have an impact on other functional and structural properties of biological communities. For instance, the progressive homogenization of habitat structure may decrease the proportion of specialist species (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006). High Nature Value (HNV) farming systems, characterized by low intensity farming and diverse, small-scale mosaics of land use types have been shown to be effective in reverting these negative effects on biodiversity (e.g. Aue, Diekötter, Gottschalk, Wolters, & Hotes, 2014; Morelli, 2013).

Here, we take advantage of a long-term breeding bird dataset on the French avifauna to investigate the processes that govern community assembly in different forest types and farmland habitats managed with a different degree of intensification. Specifically, we analyse spatial and temporal variation in the structure of local communities to address several hypotheses from a two-fold perspective, both phylogenetic and functional.

Firstly, in terms of phylogenetic structure, it has been argued that forests contain a greater proportion of evolutionarily distinctive species compared to most human-modified habitats due to its more ancient origin (Frishkoff et al., 2014). Furthermore, forests are more stable habitats, favouring the colonization and successful establishment of many clades (Dreiss et al., 2015). On the other hand, farmland habitats represent more unpredictable and stressful conditions, which may result in physiological constraints that restrict the presence of some clades in these environments (Clavel, Julliard, & Devictor, 2011). Accordingly, we hypothesize that: (1) farmland bird assemblages pose a lower phylogenetic diversity (PD) and are phylogenetically clustered, and (2) forest bird assemblages show a pattern of phylogenetic overdispersion.

Secondly, it is expected that the availability and distribution of resources largely determines the functional structure of communities (Weiher & Keddy, 1995). Under harsh or stressful conditions, environmental filtering operating on convergent traits may generate functional clustering (Cavender-Bares, Kozak, Fine, & Kembel, 2009), whereas in extremely productive habitats in which species primarily face adversity from competition, limiting similarity may favour the coexistence of species with different functional traits (Gotelli, Graves, & Rahbek, 2010; Weiher, Clarke, & Keddy, 1998). Given that forests should provide a greater availability of niches and food resources than human-modified landscapes like those resulting from agricultural practices, we predict: (3) a stronger effect of competition in forest sites resulting in functionally overdispersed assemblages; and (4) a prevalence of functional clustering in farmland sites due to the higher environmental harshness.

Thirdly, because the probability of adding new evolutionary lineages/functional groups to an assemblage decreases as assemblages become more taxonomically diverse, phylogenetic/functional diversity (FD) is expected to be positively associated with SR in a decelerating fashion (Cumming & Child, 2009; Kluge & Kessler, 2011). However, the strength of this association is expected to vary depending on the evolutionary heritage of communities and the evolutionary distinctiveness or 'originality' of species conforming a given assemblage (Pavoine, Ollier, & Dufour, 2005). As forests represent the potential natural vegetation in the temperate zone and thus, they are considered older environments than more anthropic habitats, we expect: (5) a steeper relationship (i.e. diversity level-off faster) between taxonomic and phylogenetic/FD in forest assemblages in comparison with farmland assemblages.

Finally, temporal trends in diversity at the community level are expected to mirror environmental changes and the anthropogenic influence on biodiversity (Magurran et al., 2010). In France, farmland bird populations have fallen by one third in the last two decades

(Jiguet, 2008). Reduction in effective numbers may be accompanied by a depauperation of farming bird assemblages. Meanwhile, large-scale forest maturation and afforestation have augmented in most of the Southern Europe due to increased abandonment of rural land during the last century and the restriction of agricultural practices to highly productive areas. Consequently, species associated to forested areas seem to show a positive trend (e.g. Gil-Tena, Brotons, & Saura, 2010). Based on this, we predict (6) the existence of differences in temporal trends between forest and farmland assemblages.

2 | MATERIALS AND METHODS

2.1 | Bird data

We used abundance data on breeding birds from the French Breeding Bird Survey (*Suivi Temporel des Oiseaux Communs*, STOC), a standardized monitoring program launched in 2001, in which skilled volunteer ornithologists identify breeding birds by song or visual contact each spring. Briefly, a 2×2 km plot consisting of 10-point counts -separated by at least 300 m- is randomly assigned to each volunteer. Volunteers record year after year all birds seen or heard in each of the ten sites during a 5-min period. Point counts are visited at dawn twice within three weeks around mid-May to ensure the detection of both early- and late-breeders. The maximum value of the two censuses is retained for each species as yearly abundance index. More details about the scheme and census protocols are given in Monnet et al. (2014).

We analysed data spanning a 13-year period, from 2002 to 2014. Since there exist large differences among the study plots in terms of sampled years, we only included those plots located in farmland or forest habitats that were monitored for more than 5 years in order to avoid potential biases associated to variation in sampling effort. Forest habitats comprised broad-leaved, coniferous and mixed forests, whereas farmland plots were located in areas which predominates one of the following uses according to the CORINE Land Cover inventory: non-irrigated arable land, complex cultivation patterns, agricultural land with significant areas of natural vegetation and pastures or permanent grasslands under agricultural use. In total, we gathered records from a total of 812 sites, of which 279 were located in forest habitats and 533 in agricultural land. Species with a large home range (raptors) and species that only breed in wetlands were excluded from the analysis because they are not properly monitored by the program. We also excluded species that were rarely observed and whose presence cannot be considered regular, but anecdotal (i.e. rare species). Our final data set included 107 species, which account for 99% of the total number of counted individuals (excluding raptors and water birds).

2.2 | Functional traits

A matrix of 142 traits was compiled for the 107 bird species using an extended version of the dataset described in Thuiller et al. (2014). This extensive dataset includes information on habitat, diet, life-stories, behaviour, morphology and reproduction providing a comprehensive characterization of the ecology of each species and how they interact with the environment and with other organisms (Table S1). Traits were divided into seven categories, which included both multi-trait and single-trait variables. Although we used the whole set of variables to quantify FD (hereafter 'generic functional diversity') we also computed FD indices separately for habitat and feeding traits (see more below). We paid special attention to these two subsets because they clearly asses different aspects of the niche, which defines the level of specialization of a given species (Devictor, Clavel, et al., 2010). Habitat traits reflect the environmental requirements of each species and thus, the extent to which species overlap in their use of space (Grinnellian or scenopoetic niche). Feeding traits reflect the trophic position and the guild to which each species belongs to. That is, its place in the biotic environment and the way in which each species interacts with food and other species (Eltonian or bionomic niche). These groups of traits correspond to different dimensions of the niche and thus, do not necessarily should exhibit congruent patterns over space or time (Cisneros, Fagan, & Willig, 2015).

2.3 | Phylogenetic and functional diversity indices

2.3.1 | Phylogenetic diversity

Phylogenetic diversity reflects the accumulated evolutionary history of an assemblage, and is based on the evolutionary (patristic) distance between tips in a phylogenetic tree (Faith, 1992). To determine overall PD, we computed the Faith's PD index (Faith, 1992) and associated standardized effect sizes (SES) for each of the 7,115 analysed assemblages. This index assesses species relatedness using the sum of branch lengths of the tree connecting all taxa within an assemblage. Ultrametric phylogenetic distances between the 107 species were retrieved from a Maximum Clade Credibility tree obtained from a sample of 100 dated, calibrated molecular phylogenetic trees assembled by Thuiller et al. (2011). To assess differences that may exist in phylogenetic structure between habitat types, we also computed the SES values of the mean pairwise phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD), respectively, using the independent swap algorithm (Gotelli, 2000). MNTD and Faith's PD are considered 'terminal' indices as they are a more sensitive to patterns occurring at the tips of the tree, whereas MPD is more strongly influenced by the basal structure of the phylogenetic tree (i.e. deeper branches; Mazel et al., 2016). Negative $SES_{MPD/MNTD}$ values indicate phylogenetic clustering where coexisting taxa are more related to each other than expected by chance. Negative values indicate an overdispersed phylogeny where coexisting taxa are less related to each other than would be expected at random. SES_{PD}, SES_{MPD} and SES_{MNTD} values were calculated using the R package *picante* (Kembel et al., 2010).

2.3.2 | Functional diversity

Functional diversity represents variability in ecological traits among species, reflecting the 'ecological robustness' or resilience of assemblages, which is relevant in order to assess the capacity of an ecosystem to respond effectively to global change (Villéger, Mason, & Mouillot, 2008). As an overall measure of FD, we used the Rao quadratic entropy index (Botta-Dukát, 2005), a generalization of the Simpson's index of biodiversity. Rao's index represents the average dissimilarity between all co-occurring species in the same assemblage and is greater as the number of functionally unique species increases (Laliberté & Legendre, 2010). We calculated the standardized effect size of Rao (SES_{Rao}) using the 'melodic' function (de Bello, Carmona, Lepš, Szava-Kovats, & Pärte, 2016). SES_{Rao} quantifies the number of standard deviations (SD) that observed Rao values are above or below the mean Rao of random assemblages and it has proven an accurate metric of FD (Mason, Bello, Mouillot, Pavoine, & Dray, 2013; Mouchet, Villéger, Mason, & Mouillot, 2010). Under the null hypothesis of random trait distribution in species assemblages, mean SES_{Rao} equals zero. As a result, SES_{Rao} negative values indicate trait convergence (i.e. assemblages formed by taxa sharing more similar traits than expected by chance), while positive values indicate trait divergence (i.e. assemblages formed by taxa with more distinct traits than expected at random). We tested whether annual values of FD were on average significantly different from values expected at random by means of Student's t tests, comparing observed SES_{Rao} values with the null hypothesis ($\mu = 0$; Kembel et al., 2010). In addition, we obtained a functional dendrogram to compute tree-like FD indices (mean functional distance, MFD, and MNTD) and associated SES values (SES_{MFD} and SES_{MNTD}) in an analogous way to that previously reported.

We also computed three complementary multidimensional FD metrics: functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve; Mason, Mouillot, Lee, & Wilson, 2005; Villéger et al., 2008). An interpretation of these metrics is provided in Table 1. As the trait matrix included binary and continuous trait variables, we previously performed the following steps in order to obtain a new set of 'traits' suitable to be used as input when computing the FD indices. First, a generalization of Gower's distance was employed to calculate multivariate distances between species based on the raw trait data (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). We made sure the seven trait categories had a similar weight using the 'dis.ktab' function in the R package *ade4* (Dray & Dufour, 2007). The resultant species × species dissimilarity matrix was then subject to a Principal Coordinates Analysis (PCoA) and the six first axes of this ordination were used to build a six-dimensional convex hull from which we computed FRic, FDiv and FEve using the function 'multidimFD' developed by Sebastien Villéger. We computed these three metrics from the complete matrix of 142 traits as well as separately for Grinnellian and Eltonian traits using a matrix of habitat and feeding dissimilarity, respectively. We used generalized linear mixed models (Pinheiro & Bates, 2009), in which FRic/FDiv/FEve was considered the response variable and habitat type

TABLE 1 Descriptive summary (means $\pm$ *SE*) of habitat differences in French bird functional diversities for the 2002–2014 period. Functional richness (FRic) is the amount of the functional space filled by the community; functional divergence (FDiv) measures the degree to which the abundance of a community is distributed towards the outer margins of occupied trait space and can thought of as functional 'specialization'; functional evenness (FEve) quantifies the regularity of species' abundance distribution in the functional space to allow effective utilization of the entire range of resources available

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)

the explanatory variable to test for differences between forest and farmland assemblages. Models included study year, taxonomic richness and study plot (to account for variability in the level of indices among sites) as covariates and random effect, respectively.

2.4 | Relationship between species richness and structure of assemblages

In order to explore the relationships between SR and the phylogenetic and functional structure of assemblages, we correlated mean values (averaged over years) of SR, SES_{PD} and SES_{Rao} for each of the 812 study plots by means of Pearson's correlations. We obtained similar results when considering each community as an independent sampling point (i.e. one point per community; $n = 7,115$ communities; analyses not shown).

2.5 | Temporal trends in phylogenetic and FD

We modelled bird diversity trends over the 2002–2014 timeframe to test whether forest and farmland assemblages exhibit similar temporal patterns. We considered five response variables: SES_{PD}, SES_{Rao}, FRic, FDiv and FEve. All these response variables were scaled to null mean and unit standard deviation (*z*-scores) prior to modelling in order to facilitate direct comparisons among them. We used generalized additive mixed models (GAMM; Wood, 2006) in which trends were quantified by a continuous penalized spline with a degree of

smoothness estimated by generalized cross-validation (constrained to a maximum of 4 to avoid unjustified complexity). We included study plot as random effect to account for variability in the level of indices among sites and controlled residual spatial autocorrelation with an unconstrained two-dimensional (latitude, longitude) spline. We further added taxonomic richness as a spline covariate in all models with FRic, FDiv or FEve as response variable to correct statistically the sampling-mediated positive relationship between the number of species and the trait range in an assemblage (Barnagaud, Gaüzère, Zuckerberg, Princé, & Svenning, 2017).

3 | RESULTS

3.1 | Differences in phylogenetic and functional structure between farmland and forest communities

Although farmland and forest assemblages harbour a quite similar number of breeding common species (mean $\pm$ SE; farmland: 34.54 ± 7.00, range: 11–56; forest: 32.97 ± 7.25, range: 10–56), farmland communities show a considerably higher PD in comparison with forest communities ($t = -11.07$, $p < 0.001$; Figure 1a). Annual average values of PD were significantly greater than zero in farmland assemblages throughout the study period, which suggests a prevalence of phylogenetic overdispersion in these communities (Figure 2). Instead, all annual averages for forest assemblages were negative indicating a trend towards phylogenetic clustering (Figure 2).

Accordingly, standardized effect sizes of MPD and MNTD values were lower in forest assemblages in comparison with farmland assemblages (SES_{MPD}, forest: -0.49 ± 0.71, farmland: 0.10 ± 0.38; SES_{MNTD}, forest: -0.53 ± 0.75, farmland: -0.22 ± 0.71; Figure 1a; both p-values < 0.001). In farmland communities, SES_{PD} values increased over the study period, while these showed a 'hump-shaped' pattern in forest assemblages (Figure 3a).

In terms of FD, although mean SES_{Rao} values were negative in almost all cases (Figure 2), forest assemblages showed significantly lower values in comparison with farmland assemblages (forest: -0.48 ± 0.40, farmland: -0.04 ± 0.33; $t = -19.26$, $p < 0.001$). In both habitats, temporal trends for SES_{Rao} values followed a similar pattern to that observed for PD (Figure 3a), indicating a tight correlation between both facets (farmland: $\rho = 0.27$, $p < 0.001$; forest: $\rho = 0.51$, $p < 0.001$). The obtained values for both metrics of functional structure (SES_{MFD} and SES_{MNTD}) indicated that forest assemblages exhibit a stronger signature of functional clustering (SES_{MFD}, forest: -0.39 ± 0.35, farmland: -0.11 ± 0.72; SES_{MNTD}, forest: -0.33 ± 0.39, farmland: -0.20 ± 0.70; Figure 1a; both p-values < 0.001).

Farmland communities also differed significantly from those in forests with respect to two of the three complementary FD indices; functional richness (FRic) and divergence (FDiv; Table 1). Overall, farmland communities occupy a greater amount of functional space than forest assemblages irrespective of the category to which they belong to (Figure 4). Temporal trends in FRic and FDiv for farmland and forest assemblages showed divergent patterns (Figure 3b). Trait range (FRic) and spread (FDiv) within the
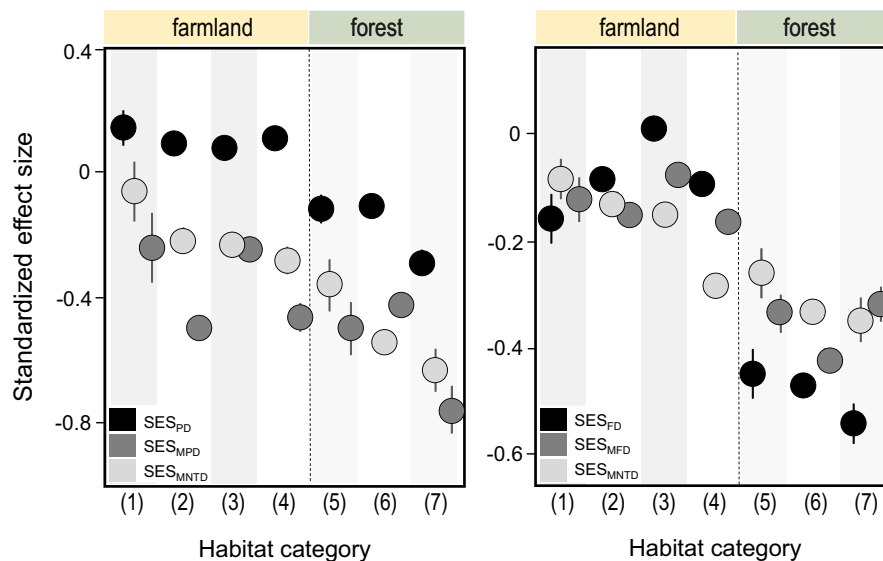

FIGURE 1 Differences in phylogenetic diversity (PD) and phylogenetic structure (left), and functional diversity (FD) and functional structure (right) among breeding bird assemblages from farmlands and forests. Bars are equivalent to confidence intervals of 95%. The two main habitat types are broken down into different habitat categories according to the CORINE Land Use classification (1: agricultural land with significant areas of natural vegetation, $n = 260$; 2: pastures or permanent grasslands under agricultural use, $n = 1,397$; 3: non-irrigated arable land, $n = 2,112$; 4: complex cultivation patterns, $n = 980$, 5: mixed forest, $n = 321$; 6: broad-leaved forest, $n = 1,559$; 7: coniferous forest, $n = 486$). SES_{PD} = standardized effect sizes of PD; $SES_{MPD/MFD}$ = standardized effect sizes of MPD/MFD; SES_{MNTD} = standardized effect sizes of MNTD (computed from both phylogenetic and functional distances). Habitat differences remained statistically significant when using raw values of PD (farmland: $1,709 \pm 277$; forest: $1,586 \pm 304$)
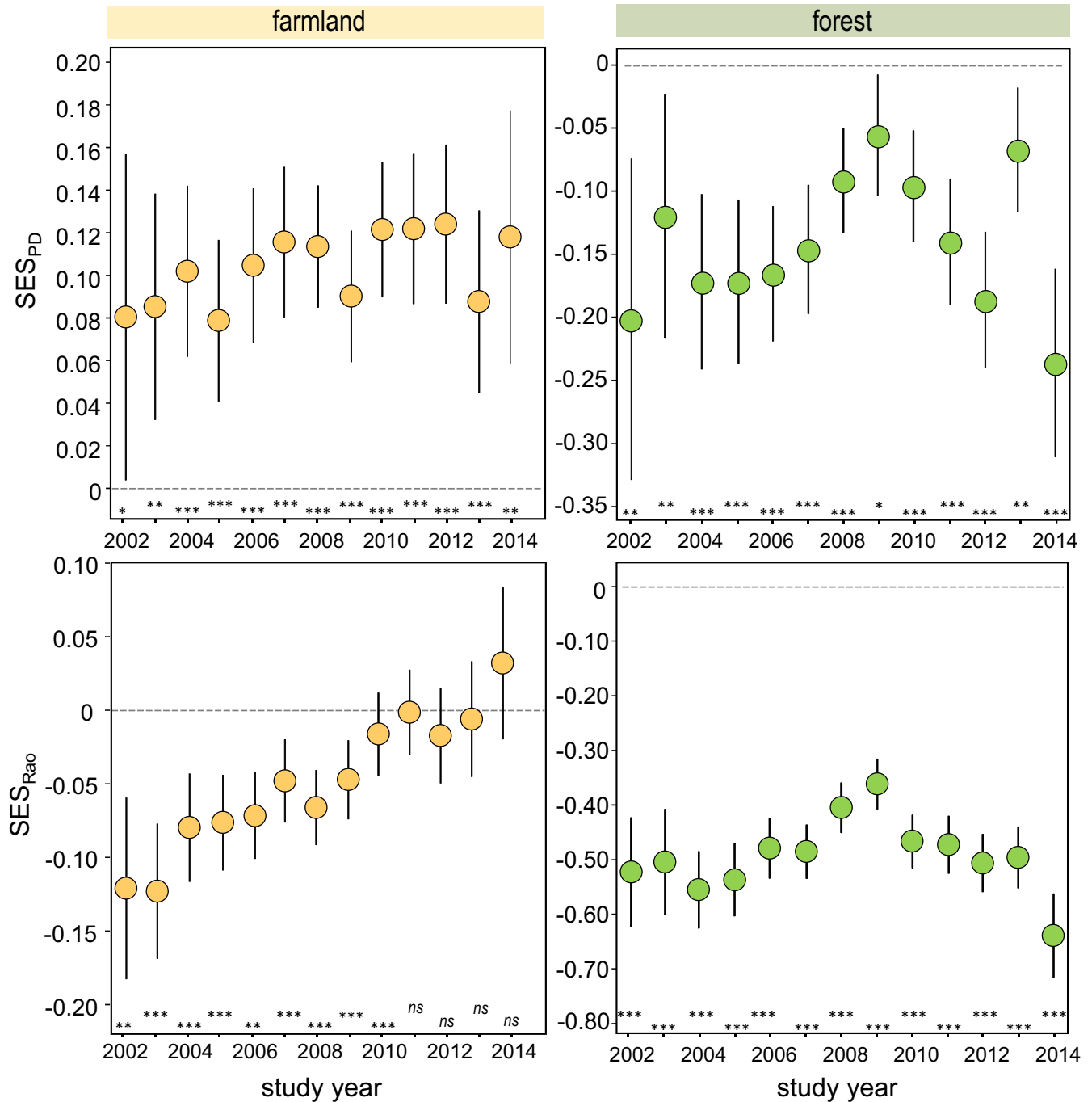
FIGURE 2 Annual mean values (±95% CI) of phylogenetic (SES_{PD}) and functional diversity (SES_{Rao}) and results of *t* tests testing whether values were significantly different from zero (*p*-values in brackets; ***: <0.001; **: <0.01; *: <0.05; *ns*: >0.05). Negative standardized metric reflects a relative clustering of species while a positive standardized metric reflects a relative overdispersion of species

functional space decreased in the forest assemblages, whereas both indices tended to increase in farmland communities. Bird assemblages appeared to become less functionally even over the study period (Figure 3b).

When grouping functional traits into different categories (subsets), we observed that, similar to generic FD, the FRic and FDiv of both feeding and habitat traits were greater in farmland

assemblages (Table 1). In contrast, the regularity of species' abundance distribution in the functional space (functional evenness) did not differ significantly between farmland and forest assemblages in either case (Table 1). It means that, although the amount of niche space filled tends to vary between farmland and forest assemblages, the way in which this space is filled does not differ between habitats.
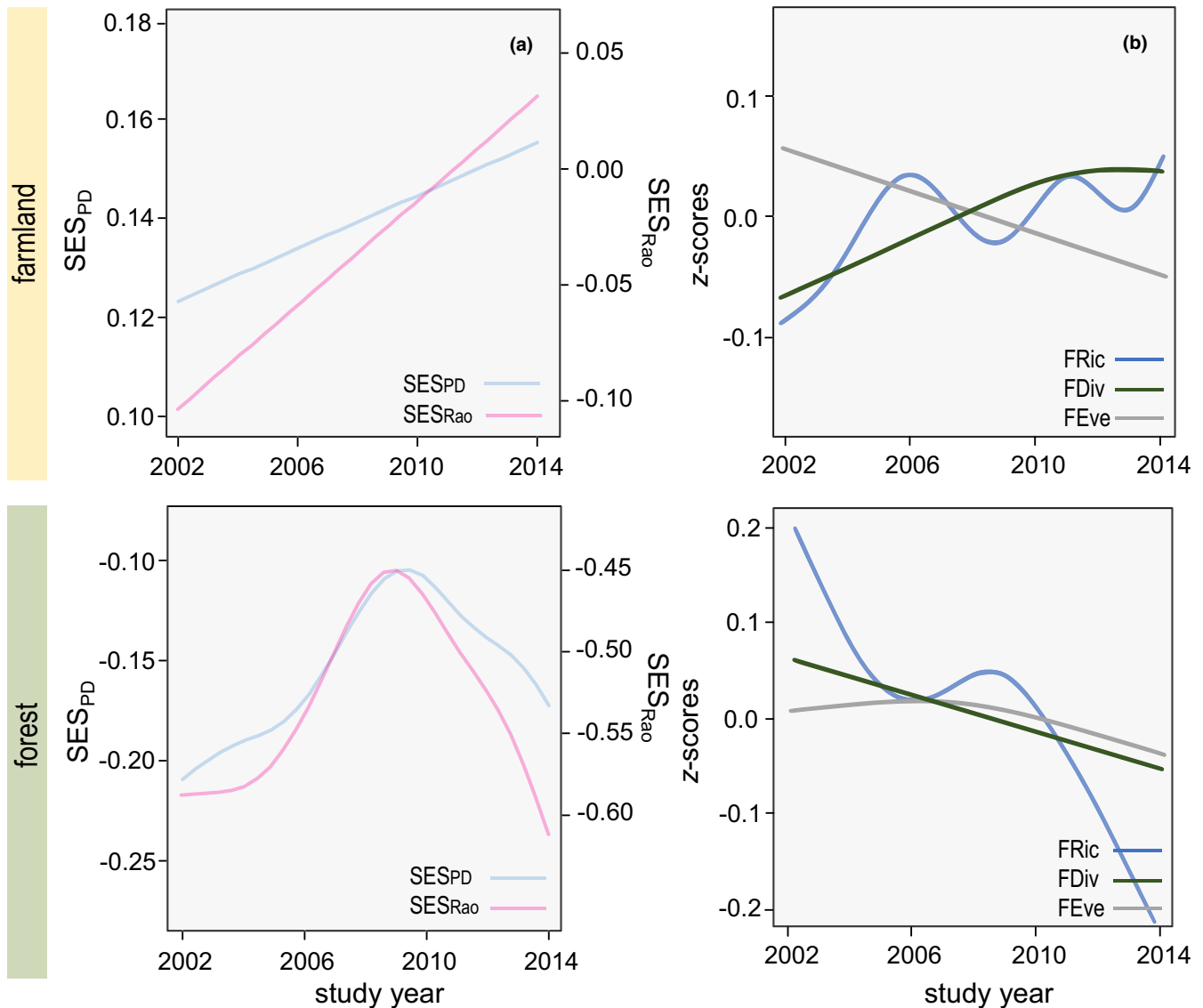
FIGURE 3 Temporal trends in (a) phylogenetic (SES_{PD}) and generic functional (SES_{Rao}) diversity, and (b) multidimensional functional diversity metrics (FRic, FDiv and FEve) over the study period (2002–2014). Trends are represented as smoothed curves fitted with GAMM. Diversity indices were scaled to mean = 0 and $SD = 1$ to ease comparisons

3.2 | Species richness versus structure of assemblages

The sign of the relationship between SR and both functional and phylogenetic structure varied between habitat categories. Both PD and FD of forest assemblages increased with increasing SR, indicating that poor assemblages were phylogenetic and functionally clustered and that random patterns have a greater influence in richer assemblages (PD: $\rho = 0.37$, $p < 0.001$; FD: $\rho = 0.38$, $p < 0.001$; Figure 5, Figure S1). In contrast, in farmland assemblages, the correlation between SR and phylogenetic and functional structure was non-significant in either case (both p-values > 0.1). Rather, the relationship turned out to be asymptotic in both cases (Figure 5, Figure S1). In fact, albeit non-significant, the model that included the quadratic term of SR provided a better fit to the data than did the model including the linear term of SR (PD, SR: 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, SR: estimate = 0.06 ± 0.26, $t = 0.23$, $p = 0.81$; SR^2: estimate = -0.43 ± 0.26, $t = -1.66$, $p = 0.09$).

4 | DISCUSSION

4.1 | Phylogenetic structure

Although it is expected that severe habitats such as savannas (Almeida, Juen, Sobral, & Dantas Santos, 2018) and agricultural landscapes (Deikumah, Kwafo, & Konadu, 2017) tend to harbour assemblages with lower PD because the persistence of some lineages is jeopardized, we found the opposite pattern; forest assemblages exhibited lower PD than those located in farmlands. This result indicates that, although farmland intensification has led to a sharp
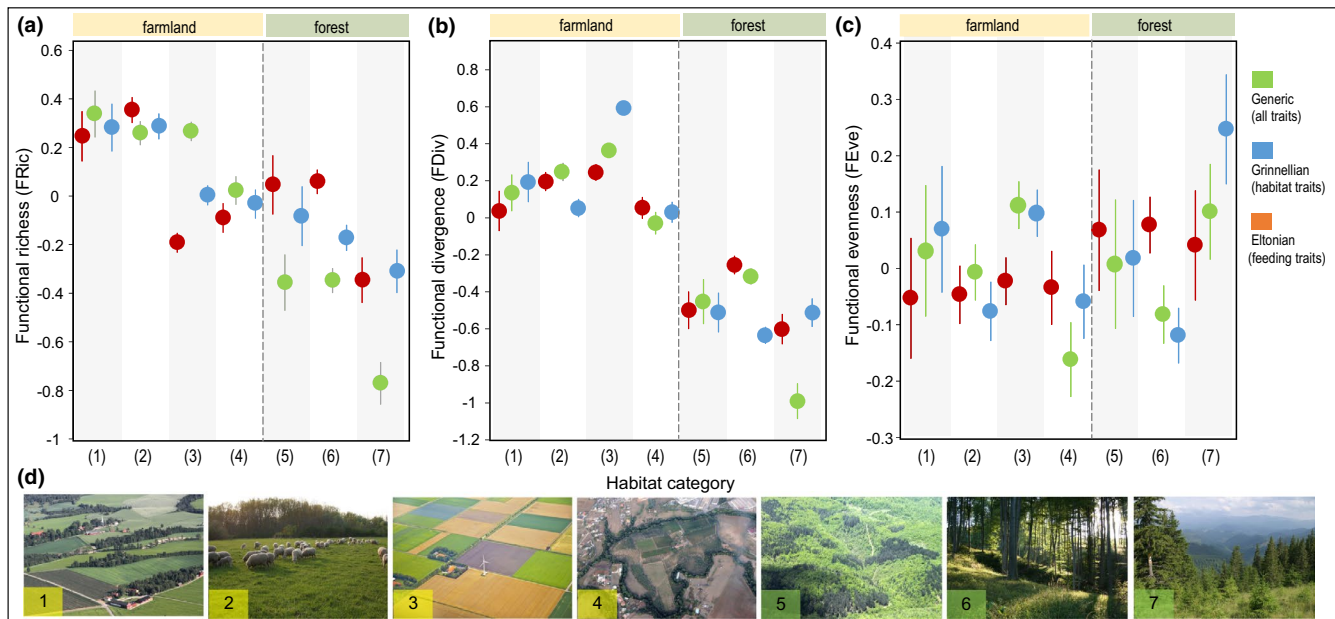
FIGURE 4 Functional diversity quantified in terms of (a) functional richness, functional divergence, and functional evenness of farmland and forest bird assemblages in France over the period 2002–2014. Values were standardized as z-cores to facilitate comparison among the different subsets. Bars represent 95% confidence intervals. The two main habitat types are broken down into different habitat categories according to the CORINE Land Use classification for illustrative purposes (see Figure 1). Pictures describing each habitat category were obtained from the Copernicus website (https://land.copernicus.eu/)

decline in populations of farmland birds, agriculture landscapes still harbour phylogenetically rich communities probably due to the legacy effects of past land use (Farina, 1997). The Mediterranean basin has experienced thousands of years of human landscape modification for livestock and agricultural purposes, with forest destruction the most obvious consequence of such an action (Blondel, 2006). As a result of traditional landscape design and management by humans, and in discordance with general assumptions on the relationship between biodiversity and habitat degradation, Mediterranean bird communities do not reach their maximum biodiversity in pristine oak woodland, but in agro-sylvo-pastoral landscape mosaics (Blondel & Aronson, 1999). In addition, it has been suggested that most of the few bird groups that differentiated within the Mediterranean region are fundamentally birds of open habitats and scrublands (e.g. *Sylvia* species; Covas & Blondel, 1998). All these factors may have contributed to the existence of a higher diversity in farmland assemblages. In this respect, it should be noted that the Mediterranean region only comprises a relatively small portion of continental France. However, traditional agroforestry systems in other French regions share key features with those typical from Mediterranean environments sensu *stricto*. For example, original *bocages*, prevalent in Western France (Atlantic zone), consist of permanent meadows used for livestock farming divided into small hedged fields interspersed with groves of trees, which provide shelter and food for a host of animals. This patchwork-like environment dating back from the Iron Age is evolving rapidly in a trend towards simplification (Pointereau & Bazile, 1995). Thus, intermediate levels of human-induced disturbance throughout civilizations seem to have contributed to keeping rural landscapes heterogeneous and promoting biological diversity.

At the present time, agricultural communities may still bear the imprint of historical landscape configurations, which is thought to persist for decades or centuries due to the lagged response of species to landscape change ('ghosts of landscape past'; With, 2007).

On the other hand, most forests in the temperate zone -including Southern Europe- are secondary forests that developed after logging of primeval forests or abandonment of agricultural lands (Blondel, 2018). Species inhabiting these forests constitute an impoverished subset of the pool of forest specialists from the Nearctic-Palearctic region, many of them being habitat generalists able to colonize a wide variety of forest environments (Covas & Blondel, 1998). Hence, Southern Europe forests would have lost most of the forest specialists a long time ago. In fact, we found that forest communities are made up of species with a lower degree of specialization than those conforming farmland assemblages (Gini specialization index; *forest*: 0.20 ± 0.03, *farmland*: 0.22 ± 0.03; see Figure S2). Such a circumstance, coupled with habitat fragmentation, could explain the existence of strong phylogenetic underdispersion in forest communities. On the contrary, the level of clustering was much lower in farmland assemblages, mostly in plots with significant areas of natural vegetation. It suggests that the presence of structural elements such as field margins, hedgerows and non-cultivated areas (small woodland patches) increases substantially the diversity of lineages that colonizes and persists in these environments (e.g. Doxa, Paracchini, Pointereau, Devictor, & Jiguet, 2012). The existence of a subtler signature of environmental filtering may have to do with the fact that domestications of animals and plants began about 4,000 years ago in this region and agriculture environments had been occupied repeatedly by phylogenetically divergent
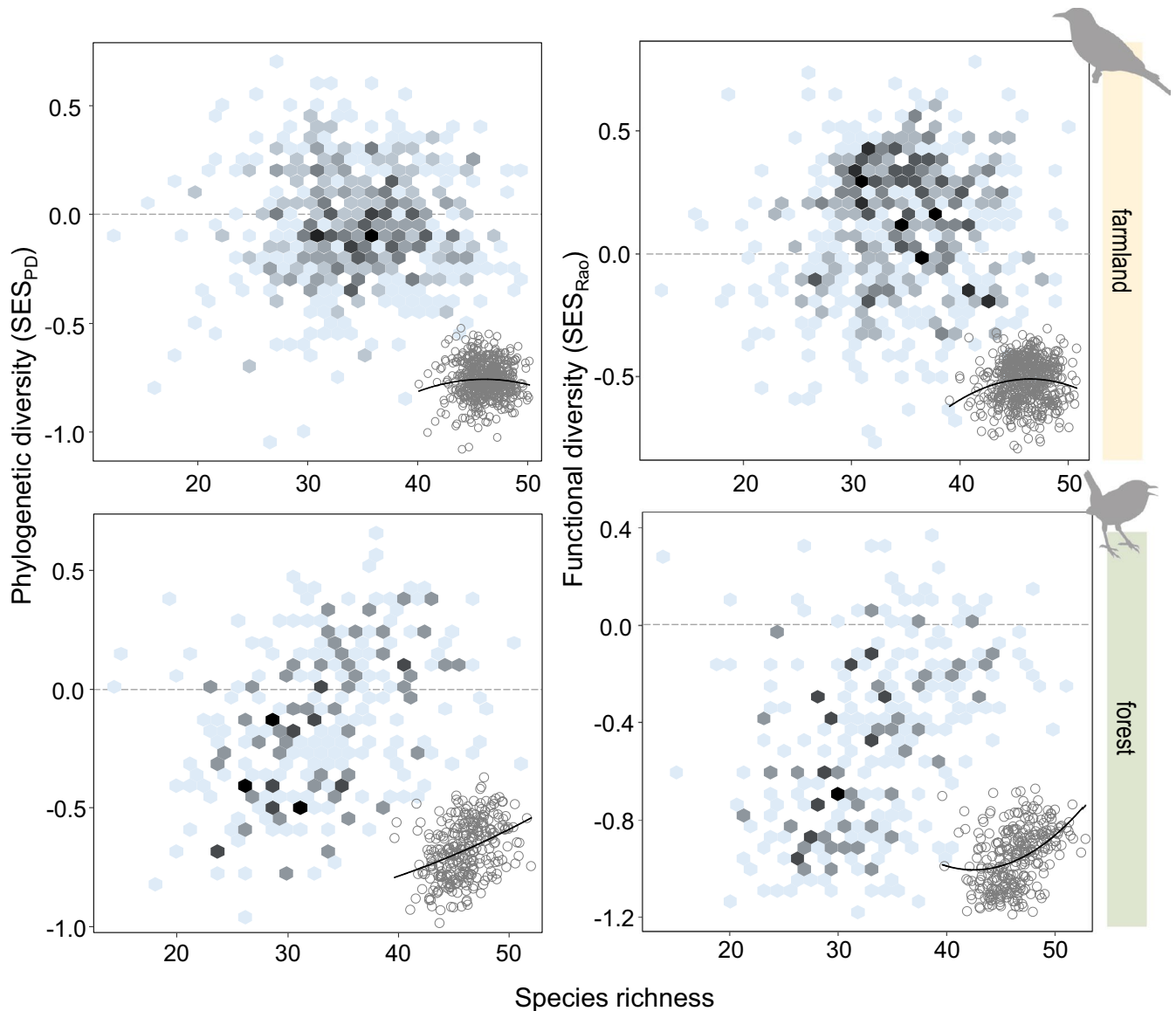
FIGURE 5 Relationship between species richness of forest and farmland bird assemblages and their respective standardized effect size (SES) of phylogenetic (Faith's PD) and functional (Rao index) diversity. Overplotting (density) of points is indicated by darker shades of gray. In the insets, polynomial functions were fitted to visualize trends in the data

lineages in multiple colonization events along its long and dynamic history (Blondel, 2006).

4.2 | Functional structure

In terms of FD, and in accordance with the phylogenetic results, we found a higher FD in farmland assemblages. A similar result has been previously observed in northern Spain (Clavero & Brotons, 2010), central Italy (Morelli, Benedetti, Perna, & Santolini, 2018) and tropical montane Ethiopia (Gove, Hylander, Nemomissa, Shimelis, & Enkossa, 2013), which indicates that bird communities in certain agricultural landscapes sustain distinct species from an ecological perspective. Whilst, in concert with that reported in terms of phylogenetic structure, forest assemblages showed a higher degree of

functional clustering, which means that they harbour a greater number of functionally similar species.

The highest values of functional richness (FRic) were found in communities from low-intensity farmlands (agricultural land with significant proportions of natural vegetation), which represent traditional land uses. At the opposite end, coniferous forests constitute the habitat type supporting the lowest values of FRic probably due to its low spatial heterogeneity in vertical and horizontal structure (Figure 4). Differences in FRic between farmland and forest assemblages were less pronounced when considering only Eltonian traits because the low richness in terms of species' feeding traits observed in communities located in lands dominated by complex cultivation patterns or non-irrigated land. It suggests a reduced trophic-niche space in the most anthropogenized and simple agricultural landscapes.

Obtained values of functional divergence (FDiv) indicate a higher degree of niche differentiation among species within farmland communities in comparison with forest communities. That is, the most abundant species in farmland assemblages are very dissimilar which may be due to -as above mentioned- limiting similarity precludes the co-existence of functionally redundant taxa, or the availability of a great variety of feeding resources (open fields for seed-eating species, bushes for frugivorous species and groves of trees for those that are canopy-gleaners) and nesting substrates in some agricultural systems. Differences in FDiv between habitats remained when analysing Eltonian and Grinellian traits separately, which implies the existence of a higher level of differentiation in farmland assemblages at different dimensions of the niche.

Regarding the way in which the biomass of the species assemblage is distributed in niche space (functional evenness, FEve), our results suggest that ecological resources are exploited in a pretty similar manner in both habitats. It means that the availability of niches potentially available but unused by the bird species of the community does not differ between farmlands and forests, a similar result to that reported by Morelli et al. (2018). According to the obtained FEve values, both habitat types exhibit a moderate uniformity of species in functional space (intermediate FEve values; Figure 4). Thus, by using functional evenness as proxy of community resilience, we hypothesize that farmland and forest assemblages are equally vulnerable to modifications (e.g., climate change or biological invasions).

In terms of functional structure, forest bird assemblages showed a pattern of clustering, contradicting our initial hypothesis of functional repulsion as result of the prevalence of limiting similarity in more benign habitats. This result agrees with that reported in forest bird assemblages from the Cerrado (Sobral & Cianciaruso, 2016) and the Brazilian Atlantic Forest (Rocha, Laps, Machado, & Campiolo, 2019). Although temperate forests are not as structurally complex and dense as rainforests from the tropical region, one possibility is that closed habitats (i.e. forests) act as local environmental filter restricting the occurrence of large birds or those that require open country (e.g. ground-feeding insectivores like pipits and larks).

4.3 | Relationship between taxonomic richness and structure of assemblages

The shape of the relationships between metrics of biodiversity and taxonomic richness differed between habitats. While in forest habitats, PD and FD increased linearly with increasing SR with no evidence of a saturating effect, within farmlands such a relationship seems to be asymptotical indicating that beyond a certain threshold (~35 spp.) both dimensions of biodiversity tend to decay (Figure 5; see also Hanspach et al., 2015). It suggests that forests are less-redundant systems than farmlands, in which an increase in the number of species not necessarily increase the FD of the community. Such a pattern

may be due to the accumulation of generalist species, which can end up displacing specialist species when the environment becomes over-saturated triggering a decline in diversity (Clavero & Brotons, 2010).

4.4 | Temporal trends

Phylogenetic and FD of farmland bird assemblages increased over the period indicating that decreasing bird abundances in agricultural landscapes are not associated with a phylogenetic impoverishment or functional homogenization of local bird assemblages. This tendency was not observed in forest assemblages, where diversity trends showed a non-linear pattern. In a similar way, multidimensional FD indices presented distinct temporal trends in both habitat types. Whereas the volume of functional space and the distribution of species within the convex hull have decreased over time in forest assemblages, these metrics tend to show a positive trajectory in farmland communities. It indicates that the drastic declines documented in bird populations across the French countryside have not led to a depaupuration of local communities in terms of PD and FD. This finding could be due to the existence of a time-lag or a decoupling between the mechanisms regulating species populations (e.g. niche processes) and community-level properties that emerge from these species, which heavily depend on biotic interactions. Hence, compensatory dynamics could explain the existence of a decrease in functional richness of forest communities despite most forest species show stable trends if, for example, increases in the populations of forest species are offset by decreases in the populations of transient species (Santini et al., 2017). In this sense, species populations and diversity indices could exhibit different responses to disturbances, which highlights the need for a better understanding of how the impacts of shifts at the species level relate to community-level descriptors (Supp & Ernest, 2014).

Lastly, a caveat of this study is that we did not account for imperfect detection of species in our analyses, a factor that may depend on the habitat type in which the survey is conducted. For instance, in a recent study, Kułaga and Budka (2019) compared the number of bird species detected through human observers (in the field) and recordings by autonomous sound recorders (manually analysed by observers in the lab) within two different habitats -forest and farmland- in Poland. They reported that observers detected more species than recorders in farmland, but not in the forest (Kułaga & Budka, 2019). Regarding this, we have to point out that although our results should be interpreted with caution, this potential bias does not affect the main findings of this study, that is, the different trajectory that farmland and forest assemblages exhibit over time.

5 | CONCLUSIONS

Several intriguing ideas for both community ecologists and conservationists arise from this study considering that agro-ecosystems

constitute one of the most common landscapes throughout the world and represent the main habitat for many bird species (Pain & Pienkowski, 1997). First, our study supports the notion that heterogeneous landscapes in which environmental conditions change significantly within short distances resulting in small-scale mosaics typical of the Mediterranean Basin and Western France, may benefit generalist species and impose limits to the potential ranges of species requiring large continuous areas of forest. Second, PD can be a surrogate for high-dimensional trait diversity and thus, by protecting more PD, we should also protect a greater amount of total FD (Faith, 2018). Third, some of the observed patterns suggest that past land use may generate strong legacy effects on biotic communities and thus, it is necessary to consider the influence of historic landscape configurations when assessing the effect that contemporary configurations have on them. Finally, and regarding this latter, community-level properties may be particularly resilient to land use alterations and thus, their accuracy as indicators of change may be limited. Consequently, gaining a better understanding of how changes at the species population level scale up to shape community properties constitutes a major challenge for biodiversity research.

DATA AVAILABILITY STATEMENT
The dataset employed in this study is available at the Dryad open-access repository (https://doi.org/10.5061/dryad.jq2bvq878).

ORCID
Vicente García-Navas https://orcid.org/0000-0002-9362-2663
Wilfried Thuiller https://orcid.org/0000-0002-5388-5274

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BIOSKETCH

Vicente García-Navas is a FCT researcher at the University of Lisbon. His work addresses how historical, phylogenetic and spatial patterns of eco-morphological and lineage diversity are influenced by biotic and abiotic factors and the interaction between them.

Wilfried Thuiller is a senior scientist at CNRS based in Grenoble. His research is focused in investigating the impacts of global change on biodiversity.

Author contributions: V.G.N. designed the study, performed the statistical analyses and wrote the manuscriot. W.T. collected the data, and contributed to interpretation of the results and writing.

SUPPORTING INFORMATION

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