Mind the gap: exploring the usefulness of historical data to assess the impacts of land-use change on bird diversity in a farmland mosaic of Northeastern Portugal (1980-2000)

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Summary

Agriculture intensification and land abandonment are the main threats to bird communities in farmlands. Although they represent the opposite endpoints of a gradient of land-use change, they are usually examined separately. In this study, we assessed the effects of the occurrence of both drivers in space and in time, on bird assemblages. The study was performed in a Mediterranean vineyard-dominated farmland mosaic located in North-Eastern Portugal, where land abandonment and

(mechanized) intensification coexisted for twenty years. The aims of this study were (1) to describe the temporal patterns of land-use change; (2) to investigate whether these changes affected the local bird species composition and ecological guild structure; and (3) to assess which species/ecological traits were more responsive to land-use changes. We compared the occurrence of birds before (1979-84) and after (2002-03) the triggering of the land-use change proccess. Results showed the prevalence of three interacting gradients of land-use change: land intensification, and direct and indirect effects of land abandonment. While the composition and ecological structure of the bird communities remained stable during the period analyzed, trait and species-specific analysis showed significant correlations with the gradients of change. This suggest that the local bird communities were able to cope with the synergic dynamics of the land-use change, possibly due to a combination of a resilient pre-change bird assemblage and the buffering effect of the competing drivers. The pros and cons of the approach adopted and the utility of past datasets as baselines to assess and monitor the impacts of environmental change on farmland bird diversity are discussed.

1. Introduction

The ongoing decline farmlands in Europe is well documented (Donald et al., 2001, 2006; Vorisek et al., 2010; Sanderson et al., 2013) and is a source of increasing concern due to the value of these human-shaped ecosystems to farmland birds, some of conservation concern (Birdlife International, 2004; Parachinni et al, 2008). This decline has been related to the effect of two contrasting land-use trends: agricultural intensification (here defined as the mechanization of the productive proccess; hereafter designed by AI) and abandonment (i.e. the cessation of agricultural management; LA) (Stoate et al., 2001, Russo, 2006; Sanderson et al., 2013).

Whilst the effects of AI on farmland birds are generally negative (Donald et al., 2001, 2006; Reif et al., 2008; Sanderson et al., 2013; Jeliazkov et al., 2016), the effects of LA are more fuzzy, as

different species are impacted differently (Russo, 2006; Herrando et al., 2014; Regos et al., 2016), according to species-specific ecological traits (Parodi et al., 2001; Sirami et al., 2007; Brambilla et al., 2010) or biogeographical origin (Suárez-Seoane et al. 2002). In fact, the loss of farmland species due to LA can be partially offset by the gain of scrubland or forest species (Russo, 2006; Keenleyside and Tucker, 2010; Herrando et al., 2014). Still, at the community level, both AI and LA are known to ultimately promote the loss or degradation of suitable habitats for farmland specialists, through changes in species composition and biotic homogenization of avian communities (Flynn et al., 2009; Clavel and Devictor, 2011; Guerrero et al., 2011).

Closely linked to the Common Agriculture Policy (CAP) (Donald et al., 2002), agriculture intensification has been observed in the most productive lowland areas of North Western Europe (Donald et al., 2001, 2006; Stoate et al., 2001). Similar trends have been described in several countries of Central and Eastern Europe after their accession to the European Union (EU) (Reif et al., 2008; Sanderson et al., 2013; Reif and Vermouzek, 2018). Conversely, LA typically prevails in less productive areas, generally in remote mountain regions (some designated as Less Favoured Areas; Merckx & Pereira, 2015), of Southern and SE Europe, where poor soils and harsh climate prevail (Stoate et al., 2009; Keenleyside and Tucker, 2010; Zakkak et al., 2015). Due to this (apparent) spatial segregation, these drivers have been examined separately in the European context. However, both land-use trends are extremes of a gradient of agricultural management whose spatial and temporal dynamics depend on the social-ecological context, and are reflected in specific landscape patterns linked to the evolution of the socio-economic pressures and thus likely to co-occur in space and in time (eg., Katayama et al., 2015).

Assessing the response of farmland birds to the impacts of land-use change is challenging, due to the complexity and long-term nature of the process. Typically, studies dealing with this research topic in Europe use regression models to relate the birds abundances (or frequency of occurrence) to relevant environmental drivers (Reif et al., 2008; Nikolov, 2010; Herrando et al.,

2014). Overall, such studies build on data on birds' abundance collected in the context of long-term censuses at national or European scales, like the Pan-European Common Bird Monitoring Scheme (PECBMS, 2019). However, required long-term data is scarce and restricted to a few European countries (Siriwardena et al., 1998; Wretenberg et al., 2007; Jiguet et al., 2012), or to specific "time windows" (Scozzafava and Santis, 2006; Sirami et al., 2008; Fonderflick et al., 2010). A common practice to overcome the absence of such data, is the usage of a "space-for-time" method, in which spatial plots in different phases of the ecological succession are surveyed at the same time and used as temporal surrogates (Moreira et al., 2001; Scorzaffava and Sanctis, 2006). Extrapolating from such data, however, must be made with care due to potential problems of site representativeness and/or non-linear bird-area relationships (Moreira et al., 2001, Bonthoux et al., 2013; De Palma et al., 2018). An increasing popular, and cost-effective, alternative is to collate data from bird atlases published in the past decades, whose utility for conservation purposes, despite known limitations, has been demonstrated (Gibbons et al, 2007; Dunn and Weston, 2008; Robertson et al., 2010).

In Portugal, data on the relationships between birds and habitat change in farmland landscapes is relatively recent compared to other countries (Delgado and Moreira, 2000; Moreira et al., 2005; Reino et al; 2010). In fact, analyses of temporal trends don't include the period of the pre-1993 CAP reform (Ribeiro et al. 2014; Santana et al., 2014, 2017). Moreover, such studies target almost exclusively High Nature Value (HNV) cereal pseudo-steppes and cork woodlands of southern Portugal, whereas the problem of AI and/or LA in the mountain farmland mosaics above the Tagus River (northern Portugal) have seldom been addressed (Moreira et al., 2001; Guilherme, 2013). We aim to fill this knowledge gap by using information from an unpublished local bird atlas performed in 1979-84 (Ferrand de Almeida, unpublished) and repeated in early 2000's (T. Múrias, unpublished data), to assess the impacts of land-use change on a typical mountain farmland bird community of northeastern Portugal.

The study area is located in the Upper Douro Wine Demarcated Region (*Região Demarcada do Douro,* RDD), the most important wine-producing region of Portugal (Andresen et al., 2005). The RDD was characterized, in large part and for a long time, by the predominance of small farms using non-mechanized methods of production (Barreto, 1992). Since the 1960's, and following a national pattern, a continuous drainage of manpower and increasing economic unprofitability led to the abandonment of production in many of these small farms. However, between 1980 and 2000, due to EU's incentives for the wine sector, many of the previously abandoned farms were reactivated or revitalized using more profitable (mechanized) agricultural management practices (Barreto, 1992). These dynamics promoted the co-occurrence of both AI and LA in space and in time, providing an excellent opportunity to explore the potential of their combined effects on the local bird communities in the study area. In this context, we postulate that the co-occurrence of AI and LA should exacerbate their respective individual effects which ultimately would be reflected as a significant loss of farmland specialists (due to AI) and a small to moderate increase in forest generalists (due to LA), with the net effect being a general impoverishment of the bird community composition.

Thus, the aims of this study were (1) to describe the space-time gradient of land-use change in the study-area between 1980 and 2000 in order to detect potential signs of the effects of both drivers; (2) to examine the potential alterations in the composition and structure of the local bird assemblages in response to the landscape change; and, (3) to investigate which ecological traits (and species) explained (if any) the adaptation of the local assemblages to land-use between 1980 and 2000. Results were discussed in the broader context of the utility of past atlas-type data (ie, presence/absence information) to establish baselines to assess and monitor the impacts of environmental change on farmland bird diversity.

2. Methods

2.1 Study area

The study area (41º15' N, 7º24' W, Figure 1A, rigth) is a Mediterranean mountainous farmland mosaic with hot summers and cold but wet winters (Ribeiro, 2000), located in the mouth of river Tua (northeast Portugal), within the limits of the Douro Wine Demarcated Region (RDD) (Figure 1A, left). Altitude ranges from 100 m near the riverbed to 600-700 m in the highest *plateaus*. The landscape is dominated by vineyards (*Vitis vinifera*) arranged in terraces bordered either by narrow schist walls (traditional vineyards), or larger earth walls (new mechanized or semi-mechanized vineyards) (Andresen et al., 2005). Other relevant cultures include traditionally managed olive-orchards, orange-groves and gardens. A variety of shrubs (*Juniperus oxycedrus* L., *Lavandula stoechas* L., *Genista* spp., *Ulex* spp. And *Erica* spp.) and native oak-type woodlands (*Quecus suber* L. *and Q. rotundifolia* Lam.) occur in the slopes leading to river Tua and its associated tributary streams, while the hilltops and middle slopes are generally occupied by pinewoods (*Pinus pinaster* Aiton). A highland wet meadow is also present in the eastern margin of the river (Figure 1B).

The human population in the study area is scarce, withthe majority of its 2000 inhabitants concentrated in eight small villages (INE, 2002; Figure 1A, left). Rural depopulation has been observed since the early 1960's (PORDATA, 2018).

2.2 Field surveys

In the context of an Atlas of Terrestrial Vertebrates carried out between 1979 and 1984 (hereafter designated as "1980"), the study area was divided in 231 500x500 m squares. From this total, a sample of 229 squares representing the main habitats described for the region (see list in Table S2, supplementary material), stratified by the relative percentage of the total area (ha), was

surveyed using the grid method described by Blondel (1969), adapted for presence/absence data (Ferrand de Almeida, unpublished). Each visit to the study area lasted from 2-7 days, distributed throughout the year, and each square was prospected at least once during the study period. A fixed census point was established in each square (centroid) and an exhaustive record of birds seen or heard was made until no new species were found. As a result, a map of the presence of each species per square visited over the six-year period was produced (Ferrand de Almeida, unpublished; see also Table S1, supplementary material). Species maps were complemented by a short description of their primary habitat(s) and (local) phenology and an abundance estimate (in a semi-quantitative scale) in the study area. The surveys led to the validation of a land cover map for the study-area including main land-use classes, based on a previous photointerpretation of 1986 aerial photos (spatial resolution 1:10.000).

Between 2002/2003 (hereafter, designated as ‘2000’) the survey was repeated replicating, as far as possible, the same plots and methodological approach (T. Múrias, unpublished data). Due to several constraints (eg. inaccessibility of some of the former plots) the number of plots visited in the second survey declined to 112, which was the final sample size used for the comparative analysis presented. Still, an effort was made to select a representative set of all habitats present.

Each square was visited at least once (but usually two or three times) over the study period. Due to the lack of evidence of seasonal-based differences in the species occurrences and distributions in 2002-2003, records gathered for each season were merged, as in the previous period. A total of 19 visits were performed between November 2002 and July 2003.

2.3. Data analysis

The raw data was tabulated in four matrices of sites (squares)-by-species (112x100) and sites-by-habitat type (112x9), two for each study period, and analysed according to the needs underlying each research aim.

2.3.1. Changes in land-use between 1980 and 2000

We spatialized the original map of Ferrand de Almeida's survey into a Geographic Information System (Qgis 2.18) and used it as the baseline information for the 1980 period. For the second survey (2000), the most updated aerial photos then available (Instituto Geográfico Português, 1994) were used to map land use types, following the nomenclature of the previous period (Table S2, Supplementary Material), to ensure comparability between maps.

The area of each land use type (in ha) was determined for the 231 squares in each period. Changes in area of each habitat for each square between 1980 and 2000 were calculated as $\Delta_{Area}=Area_{2000}-Area_{1980}$. For the purposes of this analysis, some scarce land use types shown in Figure 1B were grouped togheter (e.g., low and tall shrublands). The proportions of each land use type present in each period (Table 1) were compared with Binomial tests (Siegel and Castellán, 1988). We used the method of Chamberlain and Fuller (2000) to obtain a gradient of land-use changes between 1980 and 2000, by performing a Principal Component Analysis (PCA) on a matrix of the difference in area between periods (see above). This overcomes the problems of collinearity usually associated with multivariate data, while simultaneously allowing for a better interpretation of the results (Chamberlain and Fuller, 2000). Principal axes were derived from the correlation matrix after data reduction and centering. Only the eigenvalues >1 were taken into account; the coefficients >0.5 (rounded up) were taken as influencing the respective gradient (i.e, axis). The analysis was performed with the function 'dudi.pca', of the R package 'ade4' (Dray and Dufour, 2007).

2.3.2. Changes in the bird communities between 1980 and 2000

Species richness and ecological guild structure of the assemblage

Overall, changes in the species richness and selected guilds between 1980 and 2000 were assessed by counting the total number of species according to the: (1) phenological state in the study area (Ferrand de Almeida, unpublished); (2) biogeographic origin (Suárez-Seoane et al., 2002); (3) suitable/preferred habitat type and, (4) diet (Catry et al., 2010). Table 2 shows the levels of each category (for a more detailed description see Table S2, Supplementary Material). Significant differences in the proportion of species of each category between the two periods were assessed through chi-square contingency tables, at $p<0,05$.

Changes in composition (community heterogeneity)

Changes in the community composition between 1980 and 2000 were assessed with the model-based (GLM fits), statistic *D*. This statistic is a species-level measure of heterogeneity of occurrence (D_i) (Baeten et al., 2014). A low value of D indicates a surplus of species that are either 'rare' (present in less than half of the sites/communities) or 'prevalent' (present in half or more of the sites/communities), not contributing much to the variation within, or between, communities. The temporal variation in the metric within (or between) sites (ΔD) provides a measure of the degree of homogenization of a community (or a set of communities) along time (Baeten et al., 2014). Biotic homogenization increases if previously common species become rare and/or if some species become predominant in the community(ies) , i.e., $\Delta D_i<0$ in most sampling sites; conversely, biotic diversification increases if more species become more evenly distributed among sites: $\Delta D_i>0$. Species that contribute to $\Delta D<0$ are called 'community-convergence species'; conversely, those that contribute to $\Delta D>0$, are called 'community-divergence species' (Baeten et al., 2014). The advantage of this metric over the traditional summarized indexes of heterogeneity (e.g., Shannon's *H*) is that it pinpoints the contribution of individual species to the overall process, for instance, allowing to separate the homogenizing effects caused by species becoming prevalent from those caused by species becoming very rare (Baeten et al., 2014).

We calculated the species ΔD_i's and the community ΔD for both periods, using each sampled square as an individual "site" (A. Baeten, pers. comm.). The 'dDEV' R script, provided as supplementary material in Baeten et al. (2014) was used to calculate both metrics and their associated (permutated) p-values. As suggested by Baeten et al. (2014), we used the False Discovery Rate (FDR) method (Pike, 2011) to correct for multiple comparisons. The calculation of the FDR-adjusted p-values was performed with the function 'p.adjust', of the R base library 'stats' (R Core Team, 2019).

Response of the local farmland birds to the gradients of landscape changes

To assess the response patterns of individual species and ecological guilds to the gradients of land-use change (measured by the direction and strength of the respective correlations) we used the 'fourth-corner' approach (Legendre et al., 1997). This method combines a matrix of species abundances or presence/absence data (L) with a matrix of species 'traits' (R) and of 'environmental' data (Q), in order to find a R*Q matrix (traits*environment) expressing the contribution of each selected 'trait' to changes in species abundances or occurrence due to 'environmental' changes (Legendre et al., 1997). We used a model-based approach which employs a 'trait*environment' ('trait*env') interaction to explain species-to-species trait variation in response to environmental pressures for some link function, g(.) (Brown et al., 2014).

Two different fourth-corner models were fitted with our data. The first was a variant of the original 'trait' model with a second interaction term, species*environment ('spp*env'), using a species-specific identification variable ('spID', for the term 'spp'), to account for any residual species-to-species variation not explained by traits (model 3 in Brown et al., 2014):

$$g(p_{ij}) = b_0+b'_1(env_i)+b'_2(ssp_j)+b'_3(trait*env)_{ij}+ b'_4(spp*env)_{ij}$$

The second was the 'species-only' model, where different environmental conditions are fitted for different species, i.e., that includes only the interaction term 'spp*env' term. This model can be

considered as a fourth-corner model where the species are used as traits and is equivalent to the classic SDM approach (model 2 in Brown et al., 2014).

The models were fitted by GLM with a LASSO term included for model selection (Tibshirani, 1996). The LASSO term is a penalty that automatically sets to zero all terms in the model that do not explain any variation in response, thus simplifying the model and its interpretation (Brown et al. 2014). The first four PCA axes (i.e., gradients of land-use change) were used as the 'environmental' variables. The 'ecological traits' were the guild categories described above. The response matrix used was the one corresponding to the current bird community (ie., the 2000 period), since the objective was not to explain any local extinctions (Chamberlain and Fuller, 2000). Only species with more than 4 observations were included, and the dataset was limited to the species more likely to respond to the selected environmental gradients at the spatial scale used (mostly passerines and alike), making a total of 53 eligible species.

The analyses were performed with the function 'traitglm' of the package 'mvabund', version 4.0.1 (Wang et al., 2012), using the 'cv.glm1path' option. This method fits a sequence ('path') of GLM's with LASSO penalties using cross-validation, and returns the one that minimizes predictive log-likelihood on random test observations issued from the data set. The analysis was run twenty times, using 50:50 training/test splits. The predictive performance of the models was assessed by examining the best log-likelihoods of the respective paths.

3. Results

3.1. Changes in land-use between 1980 and 2000

The study area remained essentially an agricultural landscape in the time span covered in this work. The use of agriculture areas for active farming in the RDD, as measured by the "Utilized Agricultural Area" (UAA) (Figure 1A, lower right), presented large variations in the study period (INE, 1989, 1999); however, in Alijó and Carrazeda de Ansiães (the counties limiting the study

area), the UAA decreased only slightly, or even increased, between 1980 and 2000 (Figure 1A, lower right). In the study area only 7.0% of the agricultural land cover classes were lost, while areas classified as shrublands, woodlands and burnt areas (i.e. natural areas) increased ca 5% (Table 1). Changes in the relative area (Δ%, Table 1) of each land-use type in relation to the total area (i.e., the variation "by total area", Table 1), while statistically significant ($p<0.05$), were found to be of small (range: -0.2% to 26%). Contrastingly, changes in the area for each land-use type (i.e. the variation "by type") were, in general, more significant ($p<0.001$, range: -81.6% to +100%) .

The close correspondence between gains and losses in several land-use type classes strongly suggested the possibility of a gradient of change among, or between, the two landscape units. To clarify this, a PCA analysis was performed on the matrix of differences in area between 1980 and 200, by land-use type and square (Table 1). The first four axes accounted for 77% of the total (ie., cumulative) variance explained, with axis 1 corresponding to about 25%. Axis 1 reflected the effect of agricultural intensification - the transformation of the low-intensity vineyards to intensive or semi-intensive vineyards and, an effect of land abandonment, with traditional olive-orchards turned into shrublands. The second axis, accounting for 22% of the total variance, depicts a gradient of land abandonment in the non-agricultural areas (non-natural woodlands), by opposing pinewoods to shrublands and burnt areas. Axis 3, accounting for 19% of the variability, suggests a mixed effect of land abandonment in both the agricultural and non-agriculture areas (natural woodlands), through a substitution of traditional vineyards and cork-oak woodlands by shrublands and by other cultures, possibly (but not totally) due to indirect effects of fieldfires. Finally, Axis 4 (11.9%) shows the changes between the pinewoods and the wet meadow, possibly due to the regrowth of pine stands following the abandonment of that open area, previously used by livestock.

3.2 Changes in the bird assemblages between 1980 and 2000

Species composition and ecological structure (ecological guilds)

Overall, 100 species were recorded for the two periods considered, of which 80 occurred regularly (Table 2; see Table 2S, Supplementary Material, for details). About 80% of the species (77 out of 100) had a 'northern' (i.e., Eurosiberian) origin, with 23% Mediterranean or 'alloctonous' (African) origin. The resident species formed half of the community, and 37% were found to be migratory species (both spring and winter visitors). Approximately half of the species (48%) were characteristic of open habitats, either from natural (29%) or farmland (19%) type (categories 'Sc' and 'O', respectively), 25% were forest generalists (*sensu latu*: woodlands (18%) and shrublands (7%), categories 'Dc' and 'DS'), and 26% of the species used other habitats.

Species turnover between 1980 and 2000 was negligible, with 80% of the species common to both periods (Table 2). Also, there was no significant evidence of temporal changes in the global composition of the community according to biogeographic origin (χ^2=1.29, df=2, p<0.53), phenology (χ^2=7.62, df=3, p>0.06) or habitat (χ^2=0.15, df=4, p<0.99).

Community heterogeneity and species-specific patterns

The bird community in the study area did not show significant evidence of biotic homogenization between 1980 and 2000 (ΔD=-99.359, p<0.48, n_{sites}=112, $n_{species}$=100), but species-specific significant patterns were found. In all, 30 species presented meaningful changes in their deviances (ΔD_i's). Of these, 17 (57%) were 'community-convergent' species, while 13 (43%) were "community-divergent" species (Table 3).

The 'community-convergent' group was found to be rather heterogeneous. It included rare species that became even rarer, from several taxonomic origins and (mostly) from open/mixed habitats. (eg., *Alectoris rufa*, *Corvus monedula* (which actually gone extinct from the area), *Athene noctua*, *Sylvia undata* or *Picus sharpei)*, but also prevalent species that became more prevalent (eg., *Turdus merula* and *Fringilla coelebs)*, and also species that were rare in 1980 but became prevalent in 2000

(*Serinus serinus*, *Parus major*, *Sylvia melanocephala* and, particularly, *Erithacus rubecula*, the only confirmed case of a species that altered its phenology status in the study period, from a strict winter visitor (Ferrand de Almeida, unpublished) to resident.

The ‘community-divergent’ species, on the other hand, were all 'rare' passerine species that became less rare, and belonged to two main habitat/feeding guilds: strict woodland/shrubland species (eg., *Sylvia atricapilla*, *Troglodytes troglodytes*, *Lophophanes cristatus*, *Periparus ater*, *Certhia brachydactyla*, *Regulus ignicapillus)*, and open habitat species *sensu latu (ie. categories "O" and "Sc"* of Table 2) (e.g., *Phoenicurs ochrurus*, *Motacilla alba*, *Carduelis spp.*, *Streptopelia turtur* and *Chloris chloris)*.

Response of the local birds to the gradients of landscape changes

The model with the best predictive performance was model 2, the ’species model’ (Loglik=-2591.17 vs. LogLik=-2622.74 of model 3, the ‘traits model’). The results of the ‘traits model’ showed that habitat type, diet and biogeographic origin, by this order, were the ecological traits that best explained the response of the birds to the ecological gradients, whereas phenology was not relevant (Figure 2, left). Species of mixed diets and using open or semi-open (“Sc” category) habitats were positively associated with the gradient of agricultural intensification (PCA1), whereas species of omnivorous diets, broad biogeographic origin (ie, Eurosiberian) and “closed” habitats (“Dc” and “DS”) were negatively associated with this gradient. Species-specific characteristics (“SpID”) also contributed to explain the positive birds’ responses to this gradient. Habitat type was the only trait correlated with the gradient of abandonment in “natural” areas (PCA2). Species that used the ‘Other’ habitats responded positively to this gradient, while species of both ‘Open’ and ‘Dense Cover’ reacted negatively. The gradient of abandonment of mixed agricultural and “natural” areas (PCA3) attracted species of semi-open habitats (“Sc”), invertebrate diet and Eurosiberian origin, and was avoided by species of true open habitats (“O”). Finally, the gradient of change

between woodlands and the wet meadow (PC4) was best correlated with non-wooded habitats (“categories “O” and “Oth”) and diversified diets (omnivorous and mixed).

In the ’species model’, a total 32 species (out of 53) responded to one or several of the gradients of land use change in various combinations (Figure 2, right). The higher number of species (23) and the strong responses were related to the gradient of intensification (PC1), either positively (*Oenanthe leucura*), or negatively (*Troglodytes troglodytes, Lophophanes cristatus, Periparus ater, Aeghitalos caudatus, Columba palumbus* and *Monticola solitarius*). The species associated with the gradients of land abandonment (PCA1 to PCA4) were fewer (PCA2: 8 species, PCA3: 11 and PCA4: 13) and showed, in general, weaker responses (Figure 2, right).

The complex dynamics of land abandonment translated by PCA2 and PCA3 is reflected in the mixture of species with different habitat (and diet) requirements correlated with these axes, including open (or semi-open) habitat species like *Phoenicurus ochrurus, Motacilla cinerea* (positive correlation) and *Saxicola torquatus, P. ochrurus*, or *Oenanthe leucura* (negative correlation), and closed habitats species like *Sylvia atricapilla, Troglodytes troglodytes* and *Garrulus glandarius* (positive correlation) and *Sylvia melanocephala, Parus major, Periparus ater, Dendrocopus major*, or *Sitta europea* (negative correlation). The same consistency was found for PC4, which favoured ‘dense’ woodland species, such as *Turdus viscivorus, Luscinia megarhynchos, Garrulus glandarius* or *Certhia brachydactila*, while repelling species of scarce wooded habitats, like S*erinus serinus, Fringilla coelebs* or *Turdus philomelos.* Several species (e.g., *Troglodytes troglodytes*, *Saxicola torquatus*, *Serinus serinus*, *Phoenicuros ochruros*, *Lophophanes cristatus*, *Oenanthe leucura* or *Monticola solitarius*) responded in opposite ways to different gradients of change, suggesting that they are subjected to conflicting ecological pressures, depending on the habitats used.

4. Discussion

Land-use change is one of the major drivers of change impacting biodiversity in the Anthropocene (Newbold et al., 2015; Regos et al., 2016). Habitat destruction or landscape simplification is a major consequence of both intensification and land abandonment dynamics (Gámez-Virués et al., 2015). Its effects at the community level usually translate into a biotic homogenization, where rare specialized species are replaced by common generalists (Clavel et al., 2011; Reino et al, 2018). However, most studies focus only on land use intensification or abandonment, not providing a holistic overview of the synergic impacts of both processes on several facets of biodiversity, such as bird assemblages. Here, we combine historical and recent data on both birds and land-use patterns in a site were both drivers of change co-occurred in space and time, to try to explore the long-term correlation patterns between them, at both community and species levels.

Analysis of land use trends between 1980 and 2000 suggest that the study area remained essentially a farmland mosaic (<10% of agricultural area converted to other uses). Still, trends for intensification and land abandonment were observed (cf. Table 1). Whilst trends for intensification (cf. PCA1, Table 1) were reflected by a transformation of the traditional vineyards to intensive or semi-intensive vineyards, agricultural abandonment in the study area was reflected by a replacement of agricultural and natural areas by shrublands (cf. PCA3) and the conversion of woodlands to shrublands and burnt areas (cf. PCA2). Overall, it is possible that the competing pressures of both drivers of land-use change in the study area have counteracted their respective individual effects, preventing the emergence of a homogeneous landscape, either agricultural intensified or abandoned woodland/shrubland and contributed to maintain a heterogeneous landscape that prevailed until the early 2000's. The results observed in our study area contrasted with the patterns observed in other farmlands in northern Portugal (Moreira et al., 2001; Azevedo et al., 2011). The fact that, at the landscape-level, heterogeneity persisted, allowing the avian community to generally keep the initial diversified taxonomic and ecological species pool (a

mixture of resident farmland and woodland generalists of broad biogeographical distribution). This is a fundamental condition to preserve the functional diversity (and resilience) of the ecosystems, enabling them to resist to the effects of landscape change (Mori et al., 2013) and may explain why the associated bird communities remained so stable in terms of species composition. In fact, during the period under analysis, the region lost only two species: *Neophron percnopeterus* and *Corvus monedula*. However, these losses are probably more related to the general decline of such species in the Portuguese territory from the 1980's (Equipa Atlas, 2008), rather than to any specific features of landscape dynamics identified at the regional scale. The relative resilience at the community level seems also to be supported by the fact that no statistically significant trend of biotic homogenization in the community ($\Delta D<0$) was observed during the period under assessment .

Overall, at the intra-guild and species-specific levels, the responses obtained are clearer and in agreement with the expected effects of the two drivers of landscape change analyzed. Thus, the effects of intensification (PCA1), usually depicted as a simplification of the structural vegetation and a correspondent loss of species diversity (Stoate et al., 2009), were quite well predicted by the guild components habitat cover and diet. Conversely, the prediction of land abandonment effects was fuzzier, in accordance with the more complex nature of these changes, that affect species with a broader range of habitat and diet requirements (Russo, 2006). Nevertheless, the most visible effects of abandonment were also linked to habitat transformations, in this case into (PCA2), or of (PCA3), forested landscapes (*sensu latu, see* Table 1).

Regarding the biogeographic origin, results showed that this guild was only important to the intensification gradient, and reflected the strong avoidance of woodland species which are also broadly distributed (i.e., of Eurossiberian origin), such as *Troglodytes troglodytes, Passer domesticus, Lophophanes cristatus, Periparus ater, Monticola solitarius Columba palumbus and Aeghitalos caudatus*, for intensified (and more open) landscapes. This is in line with the findings of Suárez-Seoane (2002) who found a preference among Eurossiberian birds for more "closed"

habitats, particularly during the breeding season. The strong effect of intensification at the guild level seems to be confirmed at the species level, where a total of 23 species responded to the intensification gradient, while only 17 were related with abandonment (12 from direct and 9 from indirect abandonment).

However, analysis of individual responses were sometimes contradictory, further highlighting the complex nature of the interactions between the two drivers of change influencing patterns in the study area. For example, the occurrence of a typical "forest specialist" like *Periparus ater* was found to be negatively correlated with both intensification (PCA1) and land abandonment (PCA2), possibly reflecting impacts of loss, and degradation, of suitable woodland habitats, respectively. Such patterns are in agreement with Russo (2006), who found that, although the replacement of open habitats with scrublands or forests generally favoured forest bird species, this was not always the case, depending of the species-specific ecological requirements and the vegetation structure in the particular time series of the ecological succession.

On the other hand, *Oenanthe leucura*, an open habitat specialist and ground-feeding species that, in our study area, uses the traditional vineyards and olive-orchards (Múrias et al., 2008), showed a positive correlation with the intensification gradient (that tends to open up new feeding opportunities), and a negative correlation with direct land abandonment (PCA3), potentially due to the substitution of traditional vineyards by shrublands, which induce a loss/degradation of both feeding and nesting locations for this species (Equipa Atlas, 2008) .

In short, the results of our study suggest that the guild structure and composition of the bird communities were not strongly affected by the co-occurrence of intensification and land abandonment dynamics. Causes underlying our results may include the combination of (a) an assemblage of resilient species prior to the onset of the land-use change dynamics with (b) the buffering effect of the two competing drivers of land use change.

While these results are encouraging, given the intrinsic limitations of the dataset, the lack of information on bird abundances may be a relevant shortcoming. In fact, the distribution data alone may fail to detect subtle impacts of environmental and landscape changes, particularly at small spatial scales (Plieninger et al., 2014; Ehrlén and Morris, 2015). This inevitable caveat is linked to the characteristics of the “first generation atlas”, as is the case of our 1980 dataset, whose objective was to delimit distribution ranges and did not include abundance calculations (Keller, 2017). A related issue is the differences in sampling effort between the two study periods. While this could potentially be a problem for abundance data, we are convinced that it didn’t had a strong impact regarding the species’ occurrence and distribution. This is rooted in three aspects (a) the nature and distribution of the sampling effort: more scattered along the years in 1980, with usually a single visit per square per year (Ferrand de Almeida, pers. comm,), and more concentrated in 2000, with an average of two visits per square, (b) the sampling method used, based on the saturation of species detected per square, which ensured a maximum detection rate, and (c) the consistency in the results for both periods, both at the species and the community levels (roughly the same species present in both periods and using the same habitats).

Another potential drawback is the limited spatial resolution of the land-use map for 1984. Overall, the baseline map was obtained using aerial photos and photo-interpretation according to the standard procedures used at the time. For the more recent period, a similar procedure was adopted (see Methods), but some mismatch is expected due to differences in the spatial resolution of the imagery used to derive the information. Also, using a low resolution land use map, may have contributed to some unclear results at the species level, eg., the "preference" (positive correlation) of *Phoenicuros ochruros*, an open-habitat species, for the indirect gradient of abandonment (axis 2) which promoted a closed habitat. Still, the global consistency of the results reinforce the idea that, at least at the community level, our data resulted in reliable outcomes.

So, despite the aforementioned limitations, our research is promising as it (1) focuses on the potential synergic effect of AI and LA, either at large or small spatial scales (Sanderson et al., 2013; Katayama et al., 2015); (2) contributes to the growing number of long-term analysis of these processes in the Portuguese territory (Santana et al., 2014; Silva et al., 2018), extending them in scope (to traditional "latifundia"), space (to the northern region) and time (to the period pre-1990); and, (3) establishes a baseline for farmland birds diversity before the implementation of the first CAP revision. In fact, one of the interesting features of this study is that it allowed the recovery of a dataset that translates the potential reference situation of the farmland mosaics in the study-area in the pre-1993 CAP reform. Apart from the intrinsic value of this dataset, and considering all identified limitations, it provides a potential baseline dataset for the situation that predominated in the targeted farmland mosaics until the country entered the EU and, therefore, before the important socio-economic changes brought from the country's that impacted biodiversity and landscape patterns (Jones et al., 2011).

Coincidently, the end point of the dataset analyzed precedes the onset of the preparatory work carried out to build the Foz-Tua Dam, which begun in 2006 (Profico, 2008) and was concluded in 2017, with the reservoir flooding. The Foz-Tua Dam reservoir crosses the whole study area, and due to the spatial resolution of the data underlying this study, our results can also contribute to support future assessments of the potential direct (habitat loss) and indirect (further alterations in land-use, climatic changes) effects of the dam's implantation, by providing a long-term snapshot of the spre-dam situation in what concerns the presence and distribution of the local avian communities.

5. Conclusions

Overall, our results showed that the main gradients of land-use change detected in the area, intensification and abandonment, where reflected at the species-specific and trait-specific level, but

not at the community level. This suggests that the local bird communities were somehow able to cope with the synergic dynamics of the two contrasting drivers of land-use change.

This research is one of the few showing the potential effects of the co-occurrence of agricultural intensification and abandonment in space and in time, in recent times (e.g., Sanderson, 2013; Katayama et al., 2015; Aune et al., 2018). Although this issue has been somewhat neglected until very recently, it has the potential to increase in the future (see, eg., Katayama et al., 2015). In fact, the dynamics of the land-use changes in Europe tend to foster abandonment, thus promoting rewilding due to ecological succession in formerly abandoned areas and creating conditions to promote the co-occurrence of both drivers of change in limited spaces and times.

Finally, this study highlights that even spatially restricted, presence/absence atlas may be of value in tackling complex and modern issues related to environmental change. We hope this will foster data publication and sharing of similar unpublished datasets. In the proper context, and using appropriate analytical methods, they can still provide useful information.

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Table 1. Approximative area of each land-use type in 1980 and 2000, the variation in area (hectares) and in percentage of change between the two periods, and the gradients of land-use change (Principal Component Analysis). The shrublands were dominated mostly by *Cistus* sp., and *Genista* sp. The percentage of variation is given in terms of the relative area of each landscape type ("*by type*") and the total area of the major landscape unit were it was included (i.e., "agricultural" or "forest") ("*by total area*") occupied in 1980. Only the axis with eigenvalues >1 of the PCA are shown. Coefficients of 0.50 (rounded up) and above are depicted in bold. The proportion of the variance account for is in relation to the nine original PCA axes.

		Land-use characterization (1980 - 2000)					**Gradients of land-use change (PCA)**			
Land-use types	***Code***	***Area (ha)***		**Δ (ha)**	**Δ (%)**		**PC1**	**PC2**	**PC3**	**PC4**
		(1980)	***(2000)***		**By type**	**By total area**				
Agricultural landscapes		**2797**	**2590**	**-207.0**	**-**	**-7.4**				
Mixed traditional[1]	OV	2092	1364	-728	-34.8	-26.0	**0.779**	0.193	**0.500**	0.060
New vineyards[2]	Vin	320	1101	+781	+100.0	+27.9	**-0.824**	-0.135	-0.432	-0.163
Olive-orchards	Oli	345	117	-228	-66.0	-8.2	**-0.528**	**0.57**	0.203	0.375
Other cultures[3]	Cul	40	8	-32	-80.0	-1.1	-0.106	-0.059	**-0.502**	0.168
Forest landscapes[4]		**2262**	**2374**	**+112.0**	**-**	**+5.0**				
Pinewoodland	Pin	1101	658	-352	-34.8	-15.6	-0.085	**-0.664**	0.243	**0.658**
Oakwoodland	Cor	868	833	-35	-4.0	-0.2	-0.312	0.063	**0.626**	-0.339
Meadow	Mea	51	9	-42	-81.6	-1.9	-0.205	-0.430	0.295	**-0.540**
Shrublands	Shr	173	533	+360	+100.0	+15.9	**0.628**	**-0.527**	**-0.499**	-0.151

		Land-use characterization (1980 - 2000)					Gradients of land-use change (PCA)			
Burnt areas	Bur	69	341	+273	+100.0	+12.1	0.290	**0.820**	-0.383	-0.112
Eigenvalues			-				**2.23**	**1.97**	**1.66**	**1.07**
Variance per axis (%)			-				**24.81**	**21.87**	**18.48**	**11.92**
Cumulative variance (%)			-				**24.81**	**46.69**	**65.16**	**77.08**

[1] Traditional manned vineyards, with scattered olive-trees in old terraces
[2] Semi-intensive and intensive vineyards, mostly or fully mechanized
[3] Orchards and gardens, mainly located around the villages and farms
[4] *Sensu latu*, thatis including shrublands and other non-agricultural areas

Table 2. General characterization of the bird assemblages in the study area in 1980 and 2000, in regard to phenology, biogeographic origin and habitat type (see text for details). The total number of species (1980+2000), the number and percentage (%) of shared species and the number of species exclusive of each period and category are shown (see Table S1, supplementary material, for details on the species identities). Abbreviations as in the text.

Ecological categories	Total species (1980+2000)	Common species		Exclusive species	
		N	%	1980	2000
1. Phenology					
Resident (R)	50	47	94.0	1	2
Summer visitor (S)	20	17	85.0	1	2
Winter visitor (W)	17	12	70.6	4	1
Accidental (Ac)	13	4	30.8	7	2
2. Biogeographic origin					
Eurosiberian (E)	77	61	79.2	11	5
Mediterranean (M)	22	19	86.4	2	1
Aloctonous (A)	1	0	0.0	0	1
3. Habitat type					
Dense tree cover (Dc)	18	15	78.9	2	2
Sparse tree cover (Sc)	29	24	82.8	4	1
Dense shrublands (DS)	7	7	100.0	0	0
Open spaces (O)	19	17	89.5	2	0
Other habitats[1] (Oth)	26	17	65.4	5	4
4. All species	100	80	80	13	7

[1]Includes: natural rocky areas (4 species), natural and humanized rocky areas (5 species), riverine woodlands (5 species), ecotones (2 species) and water bodies (6 species) (according to Ferrand de Almeida, unpublished).

Table 3. Species that contributed significantly (**ΔD_i ,** $p<0.05$, adjusted for False Discovery Rate, FDR) to the compositional heterogeneity of the community between 1980 and 2000. The type of change in occurrence that contributed to the deviance is also indicated. The status of a species as "rare" or "prevalent" is based on the number of squares in which it was detected, the threshold being 56 (half of the total – see text). Table S1, in supplementary material, presents for a complete list of the **ΔD_i** and respective p-values. **PS** = Phenology Status (R = resident, W = wintering); **BO** = Biogeographic Origin (E = Eurosiberian, M = Mediterranean) (see Table 3 and Table S1, supplementary material, for details)

Species	**PS**	**BO**	**N. of squares**		**Prop. of squares**		**ΔD_i**	**Type of change/observations**
			1980	**2000**	**1980**	**2000**		
Community-convergence species								
Turdus merula	R	E	70	104	0.63	0.93	-90.551	Prevalent, more prevalent
Alectoris rufa	R	M	30	5	0.27	0.04	-89.306	Rare, more rare
Corvus monedula	R	E	13	0	0.12	0.00	-80.421	Rare, more rare
Athene noctua	R	M	12	1	0.11	0.01	-56.206	Rare, more rare
Sylvia undata	R	M	23	8	0.21	0.07	-56.094	Rare, more rare
Pica pica	R	E	16	5	0.14	0.04	-51.002	Rare, more rare
Picus viridis	R	E	35	16	0.14	0.04	-47.257	Rare, more rare
Erithacus rubecula	R/W	E	25	100	0.22	0.89	-42.660	Rare, more prevalent
Fringilla coelebs	R	E	67	90	0.6	0.80	-39.943	Prevalent, more prevalent

Turdus philomelos	W	E	49	26	0.44	0.23	-32.135	Rare, more rare
Garrulus glandarius	R	E	47	27	0.42	0.24	-28.642	Rare, more rare
Serinus serinus	R	M	50	79	0.45	0.71	-18.175	Rare, more prevalent
Parus major	R	E	49	73	0.44	0.65	-8.732	Rare, more prevalent
Sylvia melanocephala	R	M	25	90	0.22	0.80	-7.960	Rare, more prevalent
Community-divergence species								
Sylvia atricapilla	R	E	31	68	0.28	0.61	17.946	Rare, less rare
Phoenicuros ochruros	R	M	30	58	0.27	0.52	24.952	Rare, less rare
Parus caeruleus	R	E	19	52	0.17	0.46	52.701	Rare, less rare
Strepetopelia turtur	S	E	14	34	0.13	0.30	53.108	Rare, less rare
Motacilla alba	R	E	13	32	0.12	0.29	53.591	Rare, less rare
Carduelis carduelis	R	E	17	63	0.15	0.56	58.132	Rare, less rare
Regulus ignicapillus	R	E	1	14	0.01	0.13	72.968	Rare, less rare
Ttroglodytes troglodytes	R	E	12	47	0.11	0.42	76.088	Rare, less rare
Chloris chloris	R	E	12	50	0.11	0.45	77.705	Rare, less rare
Parus ater	R	E	5	27	0.04	0.24	82.854	Rare, less rare
Carduelis cannabina	R	E	5	28	0.04	0.25	85.099	Rare, less rare
Certhya brachydactyla	R	E	7	49	0.06	0.44	101.141	Rare, less rare
Parus cristatus	R	E	3	32	0.03	0.29	106.374	Rare, less rare

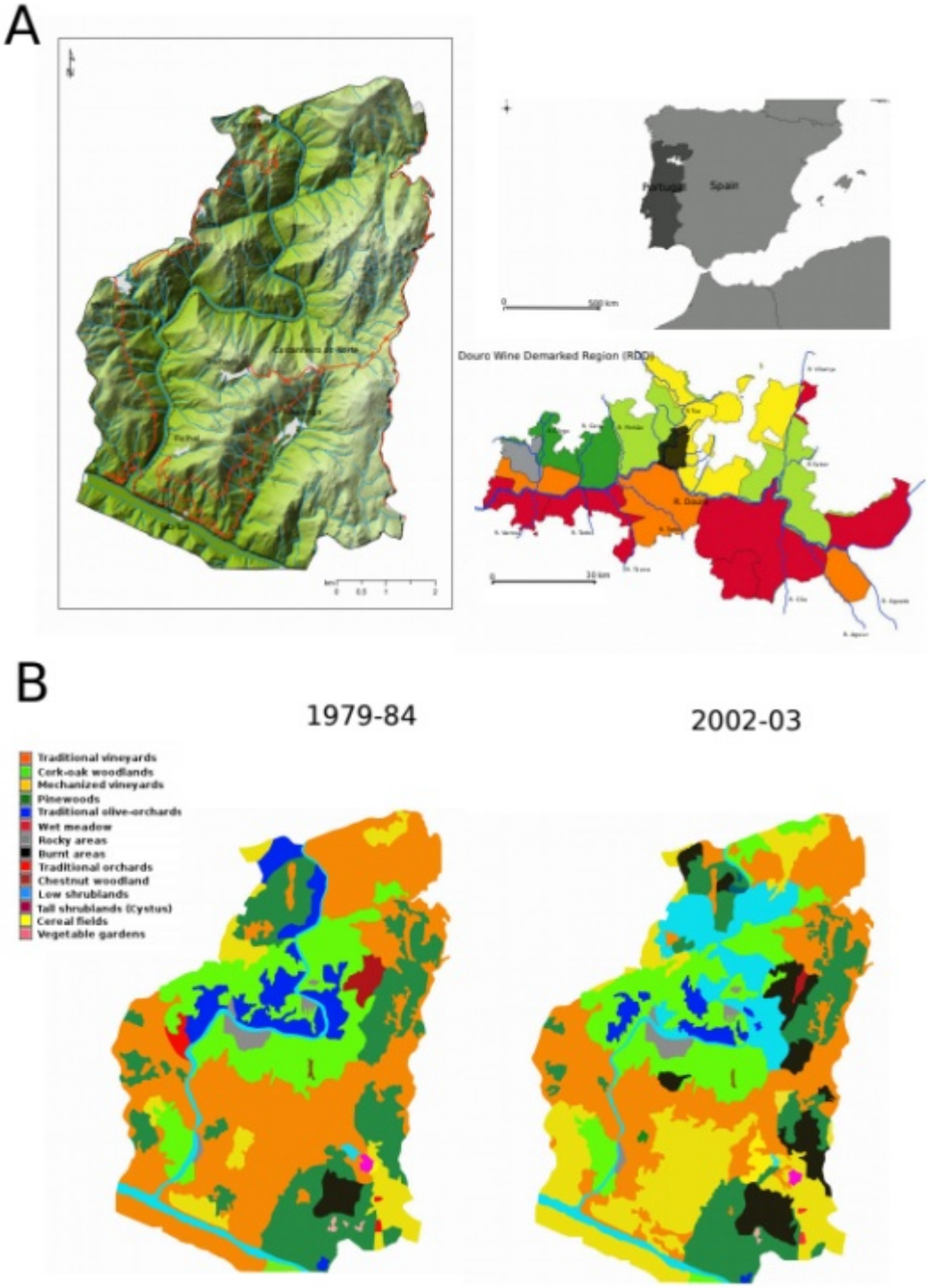

Figure 1. (A) Detailed Digital Terrain Model of the study area (left), and location of the 'Douro Wine Demarcated Region' (*Região Demarcada do Douro*, RDD) in Portugal (upper right) and of the study area in the RDD (lower right). The colours in Figure A, lower right, represent the gradient from heavy losses to medium gains in the total number of farms per ha of Usable Agricultural Area (farms/UAA) in the RDD counties between 1989 and 1999. Large decreases in the total number of farms per area (between 35% and 20% loss) are depicted in **red**; moderate decreases (19% to 10%) in **orange**; small decreases (9% to 1%) in **yellow**; no decreases or small gains (0% to 10% of gains) in **light green**; moderate gains (11% to 25%) in **dark green;** no data is available to the period concerned, in **grey.** (B) Spatial changes in land use in the study area between 1979-84 and 2002-03.

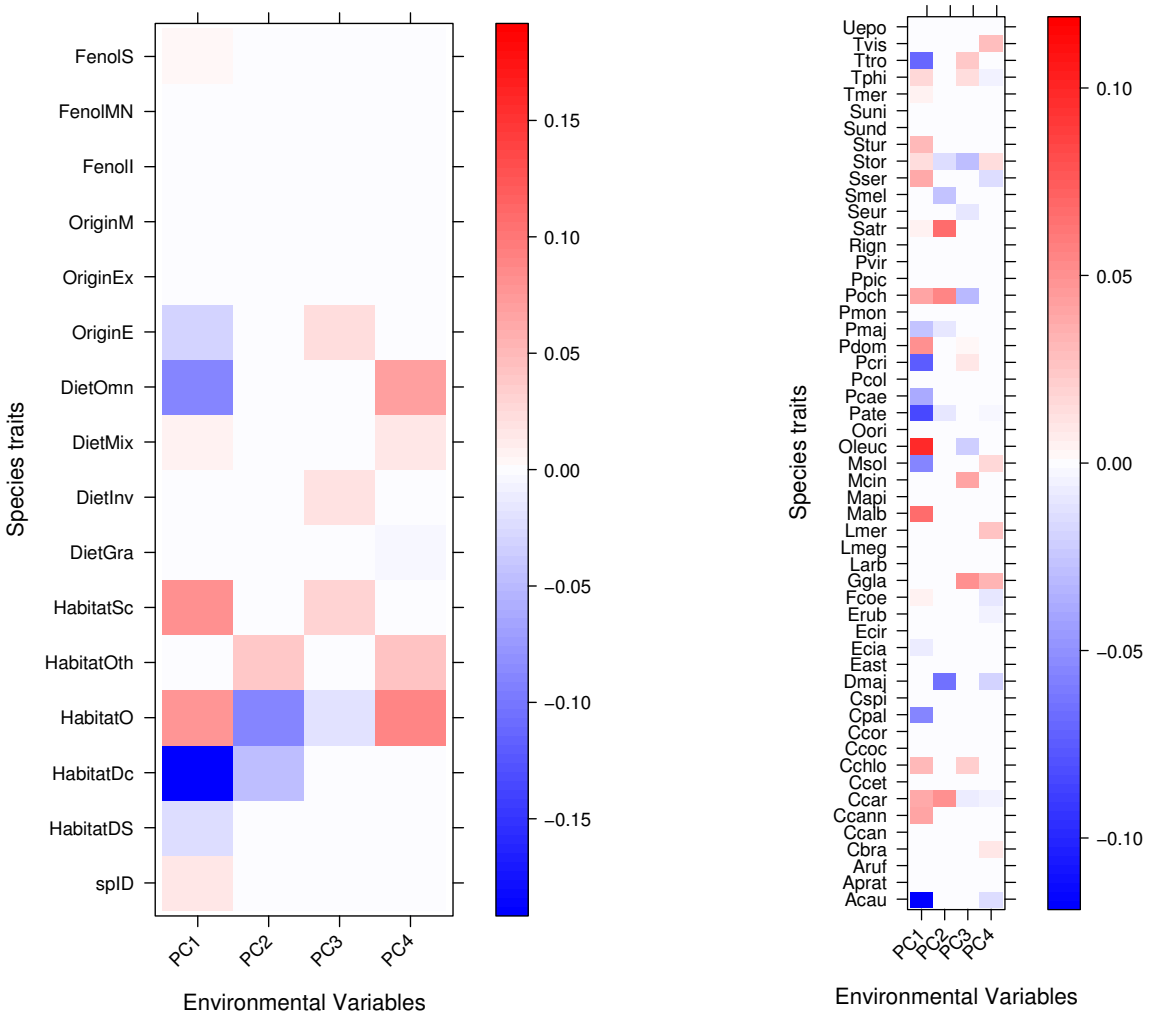

Figure 2. Graphic results of a fourth-corner analysis for the two models examined: (a) the variant of the traditional (environment*traits) model, which includes a species-specific identification term (spID) (model 3 of Brown et al., 2014), and (b) the "species-only" (i.e., environment * species) model where the trait matrix is forfeited and the species themselves are used as response (model 2) The colour gradient represents the magnitude (strength) of the coefficients retained in the model for each term (ie., pair environmental variable - response variable), from negative (blue) to positive (red) association; the darker the tone, the higher the value of the coefficient. Non-significant terms are left white. Species traits variables (model 3) are: **Fenol** - Phenology ('S': Sedentary, 'I': Wintering; 'MN': Breeding); **Origin** ('M': Mediterranean, 'Ex': Exotic (alloctonous), 'E': Eurosiberian); **Diet** ('Omn': Omnivorous; 'Mix': Mixed; 'Inv': Invertebrates; 'Gran': Granivorous); **Habitat** ('Sc': Sparse cover; 'Oth': Other; 'O': Open; 'Dc': Dense cover; 'DS': Dense shrubland); spID - Species-specific indentification. Species names codes (model 2) as in Table S1. See text for details.