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Patterns of landscape seasonality influence passerine diversity: Implications for conservation management under global change



Emilio Civantos^{a,*}, Antonio T. Monteiro^a, João Gonçalves^{a,b}, Bruno Marcos^{a,b}, Paulo Alves^a, João P. Honrado^{a,b}

^a CIBIO/InBIO. Research Center in Biodiversity and Genetic Resources, University of Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal
^b Faculdade de Ciências, Universidade do Porto, Rua do Campo Alegre FC4, 4169-007 Porto, Portugal

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ABSTRACT

The importance of environmental heterogeneity for biodiversity across scales is widely recognized in ecological theory and profusely supported by evidence. However, our understanding of the effects of spatiotemporal patterns of landscape functional properties on biodiversity is still rather limited. We examined the relationship between common passerine species richness and ecosystem functioning dynamics, namely seasonality, measured by satellite remote sensing. We focused on rural landscapes of a mountain National Park in Portugal undergoing rapid reshaping from agro-pastoral mosaics to early successional landscapes. We applied multi-model inference to compare the hypothesis of landscape seasonality as a driver of species richness with three competing hypotheses representing structural habitat heterogeneity, disturbance, and availability of food resources. We found support for landscape seasonality and its spatial heterogeneity in explaining passerine richness in mountain rural landscapes. Conversely, no significant support of the remaining hypotheses was found. These results highlight the role of ecosystem functioning variability in space and time. They also stress the importance of considering species-energy relationships for conservation at the landscape level. Specifically, they provide support and guidance to the identification of meaningful functional attributes of the landscape that shape its biodiversity. Our results further demonstrate the utility of remote sensing approaches and products to measure those attributes and follow their trends through time. Spatially-explicit measures of energy variability, such as the functional amplitude between winter and summer retrieved from earth observations, can link global socio-environmental change to species' responses and support the inclusion of landscape seasonality on conservation and monitoring frameworks.

1. Introduction

Understanding the relationship between biological diversity and landscape patterns and dynamics is crucial to face ongoing environmental change. Mediterranean landscapes of Southern Europe, shaped by human management through a combination of fire, husbandry and agriculture, sustain diverse mosaics that promote the local increase of species richness (Grove and Rackham, 2001). These landscapes typically include patches of relatively natural habitat in a mosaic of human land uses. When compared to more uniform environments, these heterogeneous landscapes allow more species to coexist locally. In fact, both species richness and diversity of bird communities were shown to be higher in heterogeneous landscapes (Benton et al., 2003; Smith et al., 2010). The importance of this heterogeneity for biodiversity across scales is widely recognized in ecological theory and supported by abundant evidence (reviewed in (Rosenzweig, 1995; Statzner and Moss, 2004).

The positive relationship between biodiversity and habitat heterogeneity at landscape scales is generally accepted, particularly in agricultural landscapes (Benton et al., 2003; Fahrig et al., 2011). The relationship between structural habitat heterogeneity and species diversity is a well-documented pattern in landscape ecology (Tews et al., 2004). Moreover, structural modifications in habitat mosaics are known to develop alongside with important changes in functional attributes of ecosystems, such as energy balance, which may ultimately affect biodiversity (Hurlbert, 2004). Therefore, in addition to structural heterogeneity, energy variations in space and time may also influence species diversity in heterogeneous mosaics, especially in dynamic landscapes submitted to driving forces such as land use change (Evans et al., 2005; Hurlbert and Haskell, 2003).

* Corresponding author.

E-mail address: ecivantos@cibio.up.pt (E. Civantos).

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Mountain landscapes in southern Europe, at the northern edge of the Mediterranean region, are undergoing rapid reshaping as the abandonment of agro-pastoral mosaics trigger secondary vegetation succession, scrub encroachment and forest re-growth (Honrado et al., 2016a). This system provides a good context not only to study the impacts of land use change on biodiversity, but also to explore the responses of biodiversity to changes in landscape functioning. Descriptors of landscape functioning dynamics, and of its temporal and spatial variability, can provide a more profound insight of the proximal landscape conditions that support biological diversity (Carrara and Vázquez, 2010; Honkanen et al., 2010; Hurlbert, 2004). This will improve our understanding of how functional and structural multi-scale landscape heterogeneity affects biodiversity, supporting better predictions of species responses to future landscape change (Orme et al., 2005), at the interface between local and regional scales (Vicente et al., 2014), thus contributing to foster conservation management and monitoring (Honrado et al., 2016b).

In this study we examined the relation between species richness of passerine birds and landscape functional dynamics namely its seasonality component as measured by satellite remote sensing. We assessed this relation in a set of mountain rural landscapes located in a National Park in Portugal and undergoing abandonment of farming and husbandry. Based on a multi-model inference (MMI) framework, we compared the predictive power of landscape seasonality with three other hypotheses representing other components of those landscapes that may influence bird species richness (habitat heterogeneity, disturbance, and availability of food resources). Finally, we aimed to outline implications for conservation management of biodiversity under land use change.

2. Material and methods

2.1. Study area

The study area comprises the mountain catchment of river Vez (252 km²), in the northwest of Portugal (Fig. 1). Parts of the catchment are included in Peneda-Gerês, the only National Park in the country, and in the Natura 2000 network of European conservation areas. During the study period (1999-2008), the average annual precipitation and temperature were 1500 mm/year and 13.8 °C, respectively. Still, annual precipitation ranged from ca. 1000 mm/year in lowlands up to ca. 3000 mm/year in highlands. Rainfall is mainly concentrated in autumn, winter and early spring, especially in the lowlands, which hold a Mediterranean type of rainfall regime. In highlands, rainfall seasonality is not so sharp and the climate is considered Temperate Atlantic with a sub-Mediterranean rainfall regime (Mesquita and Sousa, 2009). Elevation ranges from 30 to 1400 m, and slopes above 25% shape 58% of the catchment. On top of this environmental heterogeneity, humans have shaped a highly diversified and dynamic landscape that was maintained by a traditional agro-pastoral land management regime. In recent decades, however, the region has suffered marked rural abandonment, scrub encroachment and afforestation. Fire regime has changed accordingly, and wildfires are nowadays an important driver of landscape change in the region (Honrado et al., 2016a).

2.2. Data collection

2.2.1. Sampling design

A two-stage sampling design (Fig. 1) was implemented to select locations for bird counts and habitat surveys (De Gruijter et al., 2006; Köhl et al., 2006; Voříšek, 2008). This scheme accounted for two main objectives: (i) the first stage aimed to distribute sample locations across the major gradients of spatial heterogeneity and land cover/use patterns; (ii) in the second stage, the aim was to reduce the total sampling effort by concentrating surveys in smaller, representative sample units.

Thus, in the first stage a stratified random sampling approach



Fig. 1. Study area and sampling units used during field survey.

identified Primary Sample Units (hereafter PU) from a regular grid with 1 km² square units (Fig. 1). To obtain an environmental stratification of the study area for selecting PUs, four types of data layers related to environmental conditions: climate, topography, soil types, and protection regime protected areas, were combined in the Partition Around Medoids clustering algorithm (Maechler et al., 2016). Considering the Silhouette Index as the criterion to assess clustering validity and to select an adequate number of clusters (Rousseeuw, 1987), a total of six strata were obtained as the optimal solution. Based on the resulting stratification, 24 PUs were selected, with PU allocation proportional to the area of each environmental stratum and with a minimum of three PUs per stratum. In the second stage, and to reduce the costs of surveying the entire PU area, we used a systematic sampling approach to select five Secondary Sample Units (hereafter SU; with an area equal to 0.04 km²) located at the corners and the centre of each PU (Fig. 1). This spatial positioning was used to maximize the distance between SUs and avoid overlaps in bird counts. A total of 120 SUs were initially selected, but nine were not surveyed due to physical inaccessibility. For further details on sampling design see Supplementary Material - Appendix S2.

2.2.2. Bird and habitat surveys

Species richness of passerine birds was the focal response variable, and the sample plots (n = 111 SUs) were surveyed using a 100 m fixed-radius point-count approach (Bibby, 2000). Surveyed plots were separated at least by 400 m to minimize the probability of sampling the

same birds more than once. All point counts were visited once in the Spring of 2014, during the breeding season (from early May to mid-June). No surveys were performed in days with strong wind, rain or cold weather. Surveys were conducted within the first 3 h in the morning or the 2 h before sunset. All birds heard or seen inside the survey plot in a ten-minute period were recorded. Species richness was then estimated as the total number of passerine species per 10 minutes census per plot, expressing passerine community composition in each SU.

In each plot, a detailed in-field mapping of habitats was also done using the General Habitat Categories (GHCs) system and methodology (Bunce et al., 2008). In short, the identification of vegetated GHCs is based on an extended version of Raunkiaer's plant life form classification (see Supplementary Material - Appendix S1). Plant life forms are widely used to describe habitat structure (horizontal and vertical), relating it to climate, site-specific conditions and disturbance regimes. The GHC system and the supporting methodology have been tested in the field across all the environmental zones in Europe, as well as in desert biomes of several continents. Besides their adequacy to different biogeographic regions, GHCs and life form qualifiers are also used as indicators of disturbance and human management (Bunce et al., 2008). GHCs in which vegetation is not the dominant structural element are identified on the basis of "non-life forms" (urban, water, rock, etc.). In each SU, GHC parcels were mapped by an experienced botanist and a GIS expert, using a simplified version of the methodology described in (Bunce et al., 2008). The area size of the minimum mapping unit was defined as 400 m², and parcels were discriminated and mapped based on the dominance of a given GHC. All the life-form and non-life form GHCs occupying at least 10% of the parcel were recorded. In-field mapping of GHCs was carried out between May and July 2014, supported by ancillary aerial imagery.

2.3. Model development and ranking of hypotheses

2.3.1. Hypotheses and competing models

A multi-model inference (MMI) framework was implemented to test and rank the four competing hypotheses (Table 1) established to explain the observed patterns of passerine species richness. These were related to: higher habitat heterogeneity (H1) which is expected to increase species richness (Benton et al., 2003; Smith et al., 2010; Tews et al., 2004); higher landscape disturbance (H2) which is expected to decrease species richness (Moreira et al., 2001; Moreira and Russo, 2007); higher landscape seasonality (H3), expected to increase species richness (Caprio et al., 2008; Hurlbert, 2004; Hurlbert and Haskell, 2003); and higher availability of food resources (insects) (H4), also hypothesized to increase species richness (Franzblau and Collins, 1980; Poulin et al., 1994). Each hypothesis represents an attribute of the landscape mosaic that is likely to change with a shift in land management intensity, and relates to a competing model fitted with a specific set of predictors (Table 1). All four competing hypotheses were supported by previous research, scientific literature and knowledge of the study area, and they were established to avoid a blind data dredging approach to model development (Burnham et al., 2011; Dochtermann and Jenkins, 2011). Finally, a baseline 'null model', containing solely an intercept term, was also ranked to assess the predictive ability of the previous models H1 to H4.

2.3.2. Predictor variables

Five variables related with the four competing hypotheses were used to fit predictive models for passerine species richness (Table 1). Values for those variables were extracted for each SU surveyed (see Fig. 1 and sampling design).

The total number of life form and non-life form GCHs (LF) per plot was computed as a proxy of the effect of (structural) *habitat heterogeneity* on passerine diversity (hypothesis H1). Higher values of LF indicate higher structural complexity and spatial heterogeneity of local landscapes.

Burnt area (ha) was used as a proxy of *disturbance* (hypothesis H2) in mountain mosaics. Wildfires are the most important disturbance mechanism in the region (Carmo et al., 2011). The computed variable refers to the cumulative burnt area in each plot (i.e., SU) between 2000 and 2013 (14 years). The use of cumulative instead of single year values allowed accounting for the history of disturbance in the plot, with larger cumulative burnt area indicating higher incidence of disturbance and instability. This variable was computed from the Portuguese National Fire Inventory (NFI; http://www.icnf.pt/portal/florestas/dfci/inc/info-geo), a spatial dataset containing the annual distribution of burnt areas in the country.

The *landscape seasonality* hypothesis (H3) assumed that passerine species richness can be influenced by energy variability in time and space (expressed here as landscape seasonality and its spatial heterogeneity), an attribute likely susceptible to change with land abandonment. To describe this effect, two variables were defined: Functional amplitude and heterogeneity (FAH), a spatially-explicit measure of energy variability within each plot (SU) between the winter and summer seasons; and percentage of pre-breeding active farmlands (PBAF), a spatially-explicit measure of the energy spatial variability in the pre-breeding season within each plot.

FAH is a spatially-explicit measure of energy variability within each plot between the winter (December 2013) and summer (June 2014) seasons (see Fig. 2). The standard-deviation of FAH (FAH_stdv) aggregated at plot level refers to the heterogeneity of such seasonal variability within the plot. PBAF is a spatially-explicit measure of the energy variability in the pre-breeding season (March 2014) within each plot, and a potential driver of passerine richness. In the study area, during the pre-breeding season, energy variability is mostly explained by a comparatively higher photosynthetic activity in farmlands. The remaining vegetation mosaic, dominated by temperate woodlands and

Table 1

Set of hypothesis and related predictor variables hypothesized to influence passerine bird richness.

Predictor variable	Hypotheses	Temporal characteristics	References
Lifeforms and non-life forms (LF)	Habitat heterogeneity (H1) affects bird richness. Higher values of LF indicate large structural complexity and spatial heterogeneity. Large structural complexity and spatial heterogeneity increase species richness	Static	Benton et al. (2003), Smith et al. (2010), Tews et al. (2004)
Burnt area (BA)	Disturbance (H2) affects bird richness. Large burnt areas decrease species richness.	Time dependent	Moreira et al. (2001), Moreira and Russo (2007)
Functional amplitude and heterogeneity (FAH_Stdv); Pre-breeding Active Farmland (PBAF)	Landscape seasonality (H3) affects bird richness. Large energy amplitude (between winter and summer) and higher spatial variability in energy contribute to seasonality and increase species richness.	Time dependent	Caprio et al. (2008), Hurlbert (2004), Hurlbert and Haskell (2003), Seoane et al. (2013)
Suitability for Insects (SI)	Availability of food resources (H4) affects bird richness. Higher suitability for insects increases species richness	Static	Franzblau and Collins (1980), Poulin et al. (1994)

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Fig. 2. Illustration of functional amplitude and heterogeneity (FAH) variable representing the effect of seasonality hypothesis on passerine richness using three plots which registered the lowest, medium and highest variability in FAH_sdtv. On X axis is given the FAH_stdv values, while in Y axis represented the spatial attributes of the plots using true-color aerial imagery, EVI in the Summer (time 2) and Winter (time 1) season, and the monthly rate of functional change in the plot between the two seasons FAH (montly rate). Darker blue cells: lower values; darker red cells: higher values.

scrub, is concluding the winter dormancy stage (non-published data). To quantify FAH (Eq. 1), two main steps were performed. First, the Enhanced Vegetation Index (EVI, (Huete et al., 2002) was estimated using one Landsat-8 satellite scene (30 m resolution) for each season. Data were obtained from U.S. Geological Survey (USGS) through the Earth Explorer interface (http://earthexplorer.usgs.gov, Accessed 14 May 2014). Second, the Compound Interest Law (Puyravaud, 2003) was adopted to express FAH (Eq. 1). FAH is the monthly rate of functional change between winter (t_1) and summer (t_2); A₁ and A₂ represent the greenness level (EVI) at time t_1 and t_2 , respectively. If negative, FAH values correspond to a decrease in photosynthetic greenness (energy) between winter and summer, while positive values represent the



Fig. 3. Box-plots representing the predictors associated to each competing hypotheses and passerine species richness. Hypotheses: habitat heterogeneity (H1), disturbance (H2), spatial and temporal seasonality (H3), availability of food resources (H4). Predictive variables: Lifeforms and non-life forms (LF); Burnt area (BA); Functional amplitude and heterogeneity (FAH); Pre-breeding Active Farmland (PBAF); Suitability for Insects (SI).

opposite. Higher positive FAH_stdv values are associated to locations with increase in photosynthetic greenness between winter and summer seasons, but also with higher spatial variability of this feature within the plot. This may occur in plots with higher spatial heterogeneity of ecosystem functional dynamics. EVI was selected due to the ability of capturing the energy exchange dynamics in ecosystems (Huete et al., 2002) and to the known link between bird species richness and EVI at continental scale (Phillips et al., 2008).

$$FAH = \frac{1}{t_1 - t_2} ln \frac{A_2}{A_1}$$
(1)

PBAF (Eq. 2) was estimated applying a threshold (0.6) to the EVI scene based on Landsat-8 data of March 2014. This threshold separated photosynthetic active areas (EVI > 0.6) and considered all pixels above this threshold as active farmlands (AF, m^2). This map differs from traditional farmland land cover maps by considering only the farmland areas that are photosynthetically active in a specific season. Typically, active farmland crops in the pre-breeding season are related to early-spring farming practices for production of winter-spring vegetables, which may also attract birds.

Table 2

Results from model selection and multi-model inference explaining passerine species richness on Vez watershed, Portugal. The competing hypotheses are listed in descending order from the best to least fit hypothesis determined by their AICc values. Hypotheses: habitat heterogeneity (H1), disturbance (H2), landscape seasonality (H3), availability of food resources (H4). For comparison, a baseline 'null model' containing a single intercept term is used. Loglik: log-likelihood. K: number of parameters. AICc: Akaike Information Criterion value. Δ AICc: represents the differences between the AICc values of the best hypothesis considered and other hypotheses. w_i: represents the Akaike weights and indicates the probability that a particular hypothesis was best among those considered. Dev_expl: the proportion of the null deviance explained by the model. SpearmanCor: Spearman correlation index between observed and predicted values.

Hypotheses LogLik K AICc ΔAIC	w_i	Dev_expl	SpearmanCor
H3 -258,49 4,52 527,09 0,00 H4 -262,45 3,71 532,69 5,60 H1 -264,60 2,06 533,68 6,59 H2 -265,55 2,00 535,47 8,38 Null model -269,97 1,00 541,97 14,88	0,90 0,05 0,03 0,01 0,00	0,15 0,10 0,07 0,06 0,00	0,39 0,32 0,31 0,19

$$PBAF(\%) = \frac{AF}{Pa} \times 100 \tag{2}$$

Finally, the availability of food resources hypothesis (H4) assumed that passerine species richness can be determined by food availability across the landscape. To address this effect, we considered insects as a primary diet resource and used habitat suitability for insects (SI) as proxy. This variable refers to the environmental suitability of a landscape mosaic to host insects and promote their development. We assumed that such suitability would influence positively passerine species richness, since the majority of passerines in the study area are insectivorous, at least at certain times of their lives (hatchlings) (Lovette and Fitzpatrick, 2016). SI was estimated by implementing and adapting the physiological constrained model for insect suitability described in Neteler et al. (2011). A time-series of MODIS satellite land surface temperature (LST; 500 m resolution; 2001-2013 was used to estimate two processes affecting insect presence: winter egg-survival and adult annual survival (see Supplementary Material Appendix S2). In contrast to (Neteler et al., 2011), the insect life cycle step was not performed.

2.4. Statistical analyses

All variables included in the models were first standardized. Multicollinearity was then examined through Pearson pair-wise correlations to avoid including highly correlated variables. Pearson correlation coefficients and Variance Inflation Factor (VIF) values revealed that the results for the best-averaged model were not affected by multicollinearity, as correlation coefficients were always <0.4 and VIF values were <2 in all cases, which indicated no multicollinearity within competing models and supported the chosen variables and the selection criteria (Kutner, 2005).

Under each hypothesis, the response variable was related to predictor variables using Generalized Additive Models (GAMs). GAMs are flexible statistical methods that take into account the interactive behaviour of the variables (whose effects are commonly not linear) (Guisan et al., 2002). Passerine species richness (the response variable) was related to predictors by computing a Poisson distribution of errors and a logarithmic link function.

Models were ranked through the Akaike Information Criterion (AIC) with a correction for small sample size (AICc), which allows comparing models with different number of terms and complexity. We were interested in obtaining a relative ranking of each hypothesis individual effect; hence we opted not to consider combinations of different models. The model with the lowest AICc value was identified as the best

model (Burnham and Anderson, 2002), due to its highest explanatory power and support. For model comparison and ranking, we calculated the AICc difference, defined as Δ AICc = AICc initial - AICc minimum (where AICc initial is the second-order AIC of the competing model; and AICc minimum is the second-order AIC of the best model in the set). Δ AIC values provide a measure of the loss of information between a given model of the set and the best model, i.e. the strength of support for the model decreases with the increase of Δ AIC values. Models with Δ AIC < 2 are considered to have the most support. Also, if the baseline 'null model' is included in this set it means lack of fit of the competing models.

All statistical procedures were implemented in the R software (R Core Team, 2015).

3. Results

In total, 53 passerine species were recorded in the set of surveyed plots (See Supplementary Material Appendix S2), ranging from 0 to 13 per SU and with a mean of 5.84 (\pm 2.73 SD) species (Fig. 3a). The highest values were found in heterogeneous, actively managed land-scapes, dominated by mosaics of grasslands, oak woodlands and sea-sonal crops. Conversely, homogeneous landscapes occupied by early-successional vegetation and mosaics dominated by eucalypt plantations held the lowest numbers of passerine species.

The remaining box-plots in Fig. 3 (b–f) summarize the variability of the five variables related to the four hypotheses across the 111 surveyed SUs. Most SUs held low to medium habitat spatial heterogeneity (H1), with a mean LF value of 8.7 and large variability among SUs (Fig. 3b). Burnt area (H2) also showed a large variability among SUs regarding the level of fire disturbance (Fig. 3c). Cumulative burnt area three-folded the SU size in only 14 years. Regarding H3 predictors, there was also large variability in FAH_Stdv among SUs, but most of the sites presented a relatively low functional heterogeneity as expressed by seasonality values (Fig. 3d); PBAF showed again a large variability among sites (Fig. 3e). Most SUs presented PBAF values lower than 10% (small farmland extent in the sampling unit). For H4, SI varied little among SUs and almost all presented moderate suitability for insects (Fig. 3f).

The most parsimonious model explaining passerine species richness was the one expressing our landscape seasonality hypothesis (H3, Table 2). The relation between the number of species and the two predictors in this model (FAH_Stdv and PBAF) was positive (Spearman correlations were 0.26 and 0.27, respectively; Fig. 4), indicating that functional heterogeneity favours species richness of passerine birds in mountain rural mosaics. Conversely, the models expressing the effects of habitat heterogeneity (H1), disturbance (H2) and availability of food resources (H4) had considerably lower support in terms of explaining variations in passerine species richness (Table 2).

4. Discussion

4.1. Landscape seasonality as a key determinant of passerine diversity

This study revealed a primary role of landscape seasonality to explain common passerine species richness at the landscape level. This is an important finding towards a better understanding of the interactions between landscape dimensions and bird diversity, especially in mountain rural landscapes. Our results support the energy-diversity hypothesis (Carrara and Vázquez, 2010; Honkanen et al., 2010; Hurlbert, 2004), better than the habitat (structure) heterogeneity-diversity hypothesis (Tews et al., 2004), highlighting landscape energy as one of the main drivers of passerine species richness.

Here landscape seasonality expressed the difference in functional response of vegetation between winter and summer, and its interaction with land management (farming practices). This hypothesis (H3), also considers the spatial heterogeneity of seasonality; however, it reflects



Fig. 4. Relationship between passerine species richness (number of species) and the predictive variables of selected model H3. a): Functional amplitude and heterogeneity (FAH_stdv); b): Pre-breeding Active Farmland (PBAF).

heterogeneity very differently in comparison to H1, which looks into the structural complexity of vegetation and land cover. The amplitude of the seasonal change in EVI, expressed by FAH_stdv, a proxy to energy and greenness variations between the winter and summer seasons, favoured species richness of birds (Fig. 4a). Larger FAH_stdv values were associated to plots with greater functional seasonality between winter and summer, which were found in actively managed farmland mosaics with grasslands, oak woodlands, and seasonal crops (Fig. 2). The percentage of active farmlands in the pre-breeding season (PBAF) also seems to favour passerine species richness (Fig. 4b), highlighting the role of this landscape component associated to traditional farming in promoting species diversity (Moreira et al., 2005).

Overall, fewer passerine species were recorded in mosaics with lower energy seasonality and higher homogeneity in the pre-breeding season. In mountain regions of southern Europe, long traditions of lowintensity land management have promoted high levels of biodiversity (MacDonald et al., 2000). As a consequence, the local distribution and abundance of many species and habitat types in those landscapes are to some extent dependent on such low-intensity management (e.g. (Batáry et al., 2011; Santana et al., 2017). Small farms with long-term traditional management harbour high species diversity, not only due to lower nutrient and pesticide inputs (Chamberlain et al., 2000; Donald et al., 2006; Gil-Tena et al., 2015), but also due to higher landscape heterogeneity related to small-scale farming (e.g. (Benton et al., 2003)).

It is generally accepted that an increase in habitat heterogeneity has a positive influence on biodiversity (Tews et al., 2004). However, our results showed that in addition to structural habitat heterogeneity, functional heterogeneity (seasonality dynamics and the presence of active farmlands) also plays an important role in determining bird species richness. The complexity of habitats increases primary productivity and its temporal stability at the landscape level (Evans et al., 2005; Nieto et al., 2015; Oehri et al., 2017) which increases resource availability to a larger number of species (Bailey et al., 2004; Evans et al., 2005). This may partially explain why previous studies have reported contradictory results regarding habitat heterogeneity (Kleijn et al., 2006; Tscharntke et al., 2005). In the case of birds, the association between species and their habitat is largely determined by the quantity and quality of resources (functional space available to a species), and not only by the habitat per se (Boyce and McDonald, 1999; Butler and Norris, 2013).

Counter expectation, in a landscape with frequent disturbances, we found very low support for disturbance effects linked to wildfires and the availability of food resources (insects) as determinants of passerine richness. Wildfire is a recurrent disturbance occurring in our study area (Moreira et al., 2010), but landscape changes inflicted by fire may be more expressive on other diversity/abundance facets or species assemblage rather than total species richness (Dornelas, 2010). Regarding the availability of food resources, the approach to estimate landscape suitability for insects is likely prone to uncertainty since it only uses LST, and other factors may be important for explaining SI (Sjödin et al., 2008). Considering the availability of other resources besides insects might improve the support for this hypothesis, even if the majority of passerines in the study area are insectivorous, at least at certain times of their lives (Lovette and Fitzpatrick, 2016).

4.2. Implications for conservation in changing rural landscapes

Our focal mountain landscape, as many other mountain areas in Europe, is under a land abandonment trajectory (Honrado et al., 2016a), reshaping from a long-term mosaic of farmlands, grasslands and woodlands into a more homogeneous cover of early successional stages. Biodiversity relying on heterogeneous, human modified

landscapes can be affected negatively by land abandonment (Kati et al., 2010), a major land use change in many Mediterranean countries (e.g. (Butler et al., 2010; Russo, 2007; Stoate et al., 2009). Still, the effect of land abandonment on biodiversity is rather under-evaluated (Sirami et al., 2007; Suárez-Seoane et al., 2002). Our results highlight that passerine species richness may be affected by land abandonment and landscape reshaping from managed agroforest mosaics into early-successional vegetation. Efforts to consider energy-biodiversity relations in conservation frameworks may help to mitigate this effect. Implementing agri-environmental policies aimed to prevent land abandonment and halt biodiversity losses (e.g. (EEA, 2007) may also foster bird conservation while building-up socio-ecological resilience in biodiverse farmland areas (Plieninger and Bieling, 2013).

Besides their visual and acoustic conspicuous presence in the ecosystem, bird species have high ecological importance, being responsible for an important number of ecological processes amid vertebrates. Among others, they contribute to important ecosystem functions and services such as seed dispersal, pest control, pollination and nutrient deposition (Civantos et al., 2012; Sekercioglu, 2006). Our results highlight that common bird responses to landscape change as well as their consequences could be wrongly predicted if they were based solely on an assessment of structural habitat variables. Moreover, while many studies have explored the conditions during the breeding season in birds (e.g. (Butler et al., 2010; Gil-Tena et al., 2015; Santana et al., 2017), very few have considered also the wintering and pre-breeding seasons, which are critical for birds (Seoane et al., 2013; Suárez-Seoane et al., 2002). Previous studies have shown that ecological circumstances during the nonbreeding season (wintering) may affect body condition and survival rates (Siriwardena et al., 2007) and influence the dynamics of populations (Butler and Norris, 2013; Siriwardena et al., 2000).

Our study provided valuable information not only on the landscape drivers of species richness, but also on the identification of meaningful functional attributes of the landscape and on the utility of remote sensing derived variables to measure them. This has clear implications for landscape management and monitoring aimed at anticipating undesired biodiversity changes (Alcaraz-Segura et al., 2017; Gonçalves et al., 2016). In our study area, changes in seasonality may be a synthetic proxy of various environmental and landscape features and processes. Thus, remote sensing derived variables presented here might be also helpful in improving the effectiveness of monitoring schemes aimed to anticipate and early-detect species' responses to multiple interacting biodiversity drivers. Our approach can also help to prioritise sites for field assessment of multiple species and community structure (Carvalho et al., 2016), especially along the key functional gradients across landscapes and regions.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2018.07.001.

References

- Alcaraz-Segura, D., Lomba, A., Sousa-Silva, R., Nieto-Lugilde, D., Alves, P., Georges, D., Vicente, J.R., Honrado, J.P., 2017. Potential of satellite-derived ecosystem functional attributes to anticipate species range shifts. Int. J. Appl. Earth Obs. Geoinf. 57, 86–92.
- Bailey, S.A., Horner-Devine, M.C., Luck, G., Moore, L.A., Carney, K.M., Anderson, S., Betrus, C., Fleishman, E., 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. Ecography 27, 207–217.
- Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B 278, 1894–1902.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188.
- Bibby, C.J., 2000. Bird Census Techniques. Elsevier.
- Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. Trends Ecol. Evol. 14, 268–272.
- Bunce, R.G.H., Metzger, M.J., Jongman, R.H.G., Brandt, J., de Blust, G., Elena-Rossello, R., Groom, G.B., Halada, L., Hofer, G., Howard, D.C., Kovář, P., Mücher, C.A., Padoa-Schioppa, E., Paelinx, D., Palo, A., Perez-Soba, M., Ramos, I.L., Roche, P., Skånes, H., Wrbka, T., 2008. A standardized procedure for surveillance and monitoring European habitats and provision of spatial data. Landsc. Ecol. 23, 11–25.
- Burnham, K., Anderson, D., Huyvaert, K., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.
- Butler, S.J., Boccaccio, L., Gregory, R.D., Vorisek, P., Norris, K., 2010. Quantifying the impact of land-use change to European farmland bird populations. Agric. Ecosyst. Environ. 137, 348–357.
- Butler, S.J., Norris, K., 2013. Functional space and the population dynamics of birds in agro-ecosystems. Agric. Ecosyst. Environ. 164, 200–208.
- Caprio, E., Ellena, I., Rolando, A., 2008. Assessing habitat/landscape predictors of bird diversity in managed deciduous forests: a seasonal and guild-based approach. Biodivers. Conserv. 18, 1287.
- Carmo, M., Moreira, F., Casimiro, P., Vaz, P., 2011. Land use and topography influences on wildfire occurrence in Northern Portugal. Landsc. Urban Plan. 100, 169–176.
- Carrara, R., Vázquez, D.P., 2010. The species–energy theory: a role for energy variability. Ecography 33, 942–948.
- Carvalho, S.B., Gonçalves, J., Guisan, A., Honrado, J.P., 2016. Systematic site selection for multispecies monitoring networks. J. Appl. Ecol. 53, 1305–1316.
- Civantos, E., Thuiller, W., Maiorano, L., Guisan, A., Araujo, M.B., 2012. Potential impacts of climate change on ecosystem services in Europe: the case of pest control by vertebrates. Bioscience 62, 658–666.
- Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J. Appl. Ecol. 37, 771–788.
- De Gruijter, J., Brus, D.J., Bierkens, M.F., Knotters, M., 2006. Sampling For Natural Resource Monitoring. Springer Science & Business Media.
- Dochtermann, N.A., Jenkins, S.H., 2011. Developing multiple hypotheses in behavioral ecology. Behav. Ecol. Sociobiol. 65, 37–45.
- Donald, P.F., Sanderson, F.J., Burfield, I.J., van Bommel, F.P.J., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agric. Ecosyst. Environ. 116, 189–196.
- Dornelas, M., 2010. Disturbance and change in biodiversity. Philos. Trans. R. Soc. B 365, 3719–3727.
- EEA, 2007. CLC2006 Technical Guidelines. Office for Official Publications of the European Communities, Luxembourg, pp. 70.
- Evans, K.L., Greenwood, J.J., Gaston, K.J., 2005. Dissecting the species–energy relationship. Proc. R. Soc. Lond. B 272, 2155–2163.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112.
- Franzblau, M.A., Collins, J.P., 1980. Test of a hypothesis of territory regulation in an insectivorous bird by experimentally increasing prey abundance. Oecologia 46, 164–170.
- Gil-Tena, A., De Cáceres, M., Ernoult, A., Butet, A., Brotons, L., Burel, F., 2015. Agricultural landscape composition as a driver of farmland bird diversity in Brittany (NW France). Agric. Ecosyst. Environ. 205, 79–89.
- Gonçalves, J., Alves, P., Pôças, I., Marcos, B., Sousa-Silva, R., Lomba, Â., Honrado, J.P., 2016. Exploring the spatiotemporal dynamics of habitat suitability to improve conservation management of a vulnerable plant species. Biodivers. Conserv. 25, 2867–2888.
- Grove, A.T., Rackham, O., 2001. The Nature of Mediterranean Europe: An Ecological History. Yale University Press, New Haven, CT and London.
- Guisan, A., Edwards Jr, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157, 89–100.
- Honkanen, M., Roberge, J.-M., Rajasärkkä, A., Mönkkönen, M., 2010. Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. Glob. Ecol. Biogeogr. 19, 61–71.
- Honrado, J.P., Lomba, A., Alves, P., Aguiar, C., Monteiro-Henriques, T., Cerqueira, Y., Monteiro, P., Barreto Caldas, F., 2016a. Conservation management of EU priority habitats after collapse of traditional pastoralism: navigating socioecological transitions in Mountain Rangeland. Rural Sociol n/a-n/a.

Honrado, J.P., Pereira, H.M., Guisan, A., 2016b. Fostering integration between biodiversity monitoring and modelling. J. Appl. Ecol. 53, 1299–1304.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens. Environ. 83, 195–213.

- Hurlbert, A.H., 2004. Species-energy relationships and habitat complexity in bird communities. Ecol. Lett. 7, 714-720.
- Hurlbert, A.H., Haskell, J.P., 2003. The effect of energy and seasonality on avian species richness and community composition. Am. Nat. 161, 83–97.
- Kati, V., Poirazidis, K., Dufrêne, M., Halley, J.M., Korakis, G., Schindler, S., Dimopoulos, P., 2010. Towards the use of ecological heterogeneity to design reserve networks: a case study from Dadia National Park, Greece. Biodivers. Conserv. 19, 1585–1597.
- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243–254.
- Köhl, M., Magnussen, S.S., Marchetti, M., 2006. Sampling Methods, Remote Sensing and GIS Multiresource Forest Inventory. Springer Science & Business Media.

Kutner, M.H., 2005. Applied Linear Statistical Models. McGraw-Hill Irwin.

- Lovette, I.J., Fitzpatrick, J.W., 2016. Handbook of Bird Biology. Wiley.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. J. Environ. Manag. 59, 47–69.
- Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M., Hornik, K., 2016. Cluster: Cluster Analysis Basics and Extensions. R package version 2.0.5.
- Mesquita, S., Sousa, A.J., 2009. Bioclimatic mapping using geostatistical approaches: application to mainland Portugal. Int. J. Climatol. 29, 2156–2170.
- Moreira, F., Catry, F.X., Rego, F., Bacao, F., 2010. Size-dependent pattern of wildfire ignitions in Portugal: when do ignitions turn into big fires? Landsc. Ecol. 25, 1405–1417.
- Moreira, F., Ferreira, P., Rego, F., Bunting, S., 2001. Landscape changes and breeding bird assemblages in northwestern Portugal: the role of fire. Landsc. Ecol. 16, 175–187.
- Moreira, F., Pinto, M., Henriques, I., Marques, T., 2005. The importance of low-intensity farming systems for fauna, flora and habitats protected under the European "Birds" and "Habitats" directives: is agriculture essential for preserving biodiversity in the Mediterranean region. In: AR, B. (Ed.), Trends in Biodiversity Research. Nova Science Publishers, New York, pp. 117–145.
- Moreira, F., Russo, D., 2007. Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. Landsc. Ecol. 22, 1461–1476.
- Neteler, M., Roiz, D., Rocchini, D., Castellani, C., Rizzoli, A., 2011. Terra and Aqua satellites track tiger mosquito invasion: modelling the potential distribution of Aedes albopictus in north-eastern Italy. Int. J. Health Geog. 10, 49.
- Nieto, S., Flombaum, P., Garbulsky, M.F., 2015. Can temporal and spatial NDVI predict regional bird-species richness? Glob. Ecol. Conserv. 3, 729–735.
- Oehri, J., Schmid, B., Schaepman-Strub, G., Niklaus, P.A., 2017. Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. In: Proceedings of the National Academy of Sciences.
- Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Owens, I.P.F., 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature 436, 1016–1019.
- Phillips, L., Hansen, A., Flather, C., 2008. Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production. Remote Sens. Environ. 112, 4381–4392.

Plieninger, T., Bieling, C., 2013. Resilience-based perspectives to guiding high-nature-

value farmland through socioeconomic change. Ecol. Soc. 18.

- Poulin, B., Lefebvre, G., McNeil, R., 1994. Characteristics of feeding guilds and variation in diets of bird species of three adjacent tropical sites. Biotropica 26, 187–197.
- Puyravaud, J.-P., 2003. Standardizing the calculation of the annual rate of deforestation. For. Ecol. Manag. 177, 593–596.
- Core Team, R, 2015. R: A Language and Environment For Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria Version 3.2.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press.

- Rousseeuw, P., 1987. Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. J. Comput. Appl. Math. 20, 53–65.
- Russo, D., 2007. Effects of Land Abandonment on Animal Species in Europe: Conservation and Management Implications, Integrated Assessment of Vulnerable Ecosystems Under Global Change in the European Union. European Commission, Community Research, Sustainable Development, Global Change and Ecosystems, pp. 1–51 Project report.
- Santana, J., Reino, L., Stoate, C., Moreira, F., Ribeiro, P.F., Santos, J.L., Rotenberry, J.T., Beja, P., 2017. Combined effects of landscape composition and heterogeneity on farmland avian diversity. Ecol. Evol n/a-n/a.
- Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.
- Seoane, J., Villén-Pérez, S., Carrascal, L., 2013. Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods. Ecol. Res. 28, 435–445.

Sirami, C., Brotons, L., Martin, J.-L., 2007. Vegetation and songbird response to land abandonment: from landscape to census plot. Divers. Distrib. 13, 42–52.

- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P., Wilson, J.D., 2000. The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. J. Appl. Ecol. 37, 128–148.
- Siriwardena, G.M., Stevens, D.K., Anderson, G.Q.A., Vickery, J.A., Calbrade, N.A., Dodd, S., 2007. The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. J. Appl. Ecol. 44, 920–932.
- Sjödin, N.E., Bengtsson, J., Ekbom, B., 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. J. Appl. Ecol. 45, 763–772.
- Smith, H.G., Dänhardt, J., Lindström, Å., Rundlöf, M., 2010. Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. Oecologia 162, 1071–1079.
- Statzner, B., Moss, B., 2004. Linking ecological function, biodiversity and habitat: a minireview focusing on older ecological literature. Basic Appl. Ecol. 5, 97–106.
- Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe – a review. J. Environ. Manag. 91, 22–46.
- Suárez-Seoane, S., Osborne, P.E., Baudry, J., 2002. Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in northern Spain. Biol. Conserv. 105, 333–344.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8, 857–874.
- Vicente, J.R., Gonçalves, J., Honrado, J.P., Randin, C.F., Pottier, J., Broennimann, O., Lomba, A., Guisan, A., 2014. A framework for assessing the scale of influence of environmental factors on ecological patterns. Ecol. Complex. 20, 151–156.
- Voříšek, P., 2008. A Best Practice Guide for Wild Bird Monitoring Schemes. Pan-European Common Bird Monitoring Scheme (PECMBS).