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Bird taxonomic and functional responses to land abandonment in wood-pastures

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Abstract

Wood-pastures are socio-ecological systems covering vast areas in Europe. Although used for grazing and production of various forest goods, wood-pastures harbour a rich biodiversity and are usually considered as High Nature Value Farmlands. However, socio-economic pressures are driving the transformation of these valuable landscapes from multi-functional, heterogeneous habitats to homogeneous areas through either intensification or land abandonment. We investigated how changes in management intensity influence the taxonomic diversity, functional diversity and functional composition of birds in these landscapes using generalized linear models. In contrast to taxonomic diversity, functional diversity decreased significantly towards shrub-dominated and less heterogeneous areas related to the abandonment of grazing and/or understory management practices. Grassland and generalist species, and associated guilds such as granivores, ground-nesters and ground-foragers are almost absent less managed areas. On the other hand, shrub-dominated areas favour forest species, particularly understory/canopy foragers and arboreal nesters, although the forest guild is still well-represented in actively managed, heterogeneous areas. Our results indicate the abandonment of wood-pasture management affects the prevalence of grassland and generalist species, leading to functional diversity loss and potentially reduced ecosystem functioning. We suggest non-intensive, active management is needed to maintain habitat heterogeneity and canopy openness, enhancing trait diversity in wood-pastures.

Keywords: functional diversity; breeding birds; wood-pasture; management intensity; montado/dehesa; socio-ecological systems

1. Introduction

Wood-pastures are social-ecological landscapes that have been shaped by various land-use regimes prevailing in much of Europe (Hartel and Plieninger 2014). They usually have high economic value provided by a multi-functional management that may include livestock grazing, cork extraction, timber production, crop cultivation and tree pruning for firewood and charcoal (Moreno et al. 2018). Many wood-pastures conciliate economic value with the maintenance of rich biodiversity, and as such are considered High Nature Value Farmlands (Pinto-Correia and Ribeiro 2012). This richness is particularly evident in wood-pasture landscapes which are spatially heterogeneous due to the availability of habitats such as riparian galleries, hedgerows, shrubby patches and olive orchards (Leal et al. 2016; Oksuz et al. 2020). The maintenance of the multiple values of wood-pastures depends on a balanced management of the landscape (Plieninger et al. 2015). However, recent social and economic changes in Europe are transforming traditional wood-pasture management through intensification or abandonment (Bergmeier and Roellig 2014), putting the balance between natural and economic values at risk.

Land-use intensification induces habitat homogenization and causes biodiversity loss in wood-pastures (Flynn et al. 2009). Land abandonment also affects many wood-pastures (Godinho et al. 2016) although its consequences are comparatively less studied than intensification (Estel et al. 2015). Land abandonment, which may have natural (Rey Benayas et al. 2007) and socio-economic drivers (Levers et al. 2018), often leads to areas with little use beyond extensive grazing or even a complete ceasing of all exploitation, resulting in less heterogeneous habitats with dense shrubby vegetation (Rey Benayas et al. 2010). These landscape changes can influence biodiversity and ecosystem processes, although the effects vary depending on the taxon and geographical region (Queiroz et al. 2014). For instance, the loss of open areas can reduce habitat heterogeneity and, consequently, the diversity of feeding and nesting resources for birds (Sirami et al. 2009). The subsequent loss of bird species changes the trait composition of assemblages, which may in turn affect ecosystem functioning and services (Hooper et al. 2005). Thus, assessing how trait composition responds to land abandonment, particularly those traits that simultaneously influence species responses and functions (i.e. “response and effect traits”; Luck et al. 2012; Díaz et al. 2013), can reveal how biodiversity and ecosystem functions may be affected by this type of land use change (Mouillot et al. 2013). This knowledge is crucial to inform managers and decision-makers about potential negative consequences of such changes and to develop adequate strategies to minimize them (Wood et al. 2015).

In this study, we aimed to explore how changes in habitat structure driven by different management intensities influence bird taxonomic diversity, functional diversity and trait assemblages in wood-pastures across the Iberian Peninsula and North Africa. Birds, being good indicators of environmental change (Sekercioglu 2006), are likely to represent key ecosystem services in wood-pastures, including seed dispersal, pest regulation or pollination (Pons and Pausas 2007; Ceia and Ramos 2016). We related taxonomic and functional indices to habitat structure, characterized by a set of variables including understory cover and height, tree density and habitat heterogeneity, as indicators of a management intensity gradient ranging from active management towards land abandonment. Specifically, we aimed to answer the following questions: i) How do changes in management intensity gradient influence the taxonomic and functional diversity of birds in wood-pastures? ii) Which specific traits drive the responses of birds to the habitat along the management intensity gradient?

2. Methods

2.1 Study Area

Our study encompassed much of Portugal, Spain and Morocco, in areas dominated by a wood-pasture system distributed across the western Mediterranean, known as *montado* in Portugal, *dehesa* in Spain and *azaghar* in some regions of North Africa (Fig. 1). The woody plant composition of the sampled areas is dominated by cork oak (*Quercus suber*), sometimes co-occuring with other oaks (e.g. Algerian oak *Q. canarensis*, holm oak *Q. rotundifolia*, Pyrenean oak *Q. pyrenaica*), pine trees (e.g. stone pine *Pinus pinea*, maritime pine *P. pinaster*), and other tree and shrub species (e.g. mastic tree *Pistacia lentiscus*, wild olive trees *Olea europaea* var. *sylvestris*, strawberry tree *Arbutus unedo*, etc.). The most common management practices in the study area are livestock grazing with various degrees of intensity, cork extraction, cropping and pruning (Berrahmouni et al. 2007; Moreno et al. 2018). Moderate to intensive grazing is prevalent in lowland wood-pastures, whereas shrub encroachment tends to occur in more rugged areas (Bugalho et al. 2009; Bugalho et al. 2011). The annual average temperature ranges between 11-18°C and the annual rainfall is 410-910 mm in the study area (http://www.worldclim.org/).

Fig. 1 Map of the study areas located in Portugal, Spain and North Africa. Circles represent the sampled wood-pastures in Portugal (N=17), Spain (N=13) and in Morocco (N=7).

2.2 Bird sampling

Bird sampling was performed during the spring of 2011 using five-minute bird point counts (Bibby et al. 2005). In total, thirty-seven wood-pastures with a minimum of 50 hectares and at least 10 km apart, were sampled across Iberia (17 in Portugal, 13 in Spain) and North Africa (7 in Morocco). We were able to investigate the biodiversity patterns of birds across Europe and North Africa given the similarity of the bird species assemblages in both Europe and North Africa wood-pastures (Correia et al. 2015a). Fifteen sampling stations were set up in each of these wood-pasture areas, at least 200 m apart and 100 m or more from the edge. Each station was visited twice, once during the early half (1 April to 15 May) and once during the late half (16 May to 20 June) of the breeding season. The same observer performed all the counts, always during periods of peak bird activity (controls in the morning and in the late afternoon for each area) and avoiding rainy and windy conditions and areas recently harvested for cork (Godinho and Rabaça 2011). All birds detected visually or acoustically were recorded and their distance to the observer was estimated. Birds detected more than 100 m away from the observer and over-flying birds were excluded from the analysis since they may not be relevant to the studied habitat. The total abundance of each species in each area was defined as the maximum sum of individuals detected in the fifteen counting stations for any of the two controls, as this represents the minimum number of birds present in that area (Bibby et al. 2005). Bird abundance data is presented in Online Resource 1.

2.3 Trait data

We obtained data on six response and effect traits (Luck et al. 2012; Hevia et al. 2016) for 54 recorded species to analyse the functional diversity and functional composition of bird assemblage. The traits considered for analysis include: habitat guild, feeding guild, foraging strata, nest type, wing aspect ratio and body mass (Online Resource 2). These traits were selected based on a priori hypotheses regarding their role in determining bird responses to habitat structure (Online Resource 3).

2.4 Environmental data

Habitat structure was characterized with a set of variables including understory cover and height, tree density and habitat heterogeneity (Online Resource 4). These habitat variables were estimated in the same circle plots where bird census was performed. These variables were selected as indicators of a management gradient ranging from areas with active human management (e.g. regular grazing, shrub removal) to sparsely used areas (e.g. occasional grazing, no shrub removal) resembling a process of land abandonment. Herb cover and shrub cover (% of ground cover), herb height (in 5 cm classes up to 25 cm) and shrub height (in 25 cm classes up to 150 cm) were visually estimated by the same observer. Tree density (number of trees per hectare) and canopy cover (% ground cover covered by tree crowns) were estimated visually using aerial images available from Google Earth v7.1 for the year 2011. A habitat heterogeneity index was obtained using six variables; herb cover, herb height, shrub cover, shrub height, tree density and canopy cover applying the formula of “max.value–min.value/mean value” for each habitat variable. The resulting values were summed to obtain a single heterogeneity value for each wood-pasture (Rotenberry and Wiens 1980). Finally, we performed a Principal Components Analysis (PCA) combining variables of herb and shrub cover, herb and shrub height, tree density and habitat heterogeneity to reduce the number of variables and avoid collinearity (Dormann et al. 2013). The first and the second axis of the PCA were used to represent the main habitat management gradients in the subsequent analysis (Table A1, Online Resource 5). The first PCA axis mostly represents ground vegetation structure ranging from actively managed herb dominated and more heterogeneous areas to shrub dominated and less heterogeneous areas, where the management intensity is lower. The second PCA axis represents a gradient from sparsely treed and heterogeneous areas to densely treed and less heterogeneous areas.

Shrub cover and height are lower in these densely treed areas due to more intensive management. (Figure A1, Online Resource 5).

2.5 Data Analysis

We estimated bird taxonomic diversity using species richness and the Shannon diversity index, and estimated functional diversity with multi-trait functional richness (FRic), functional dispersion (FDis) and functional evenness (FEve) indices (Villéger et al. 2008). Before each index was calculated, we assessed the correlation between traits using Spearman correlations to avoid biases in calculation of functional diversity indices (Lepš et al. 2006). There were no correlations between traits (p>0.05), so they were all included in calculations and given equal weight. We also calculated the community weighted means (CWM) index of each trait to test how individual trait composition responded to changes in habitat structure.

All analyses were performed in R, version 3.5.2 (R Core Team 2019). Species richness and Shannon index were calculated using the "vegan" package (Oksanen et al. 2016), and functional diversity and functional composition indices with package "FD" (Laliberté et al. 2014). Later, we tested the relationship between biodiversity indices and the management intensity gradients represented by PCA axes using generalized linear models. Adjusted R-squared values were calculated for each model using "rsq" function in "rsq" package (Zhang 2018). Additionally, we performed a Detrended Correspondence Analysis (DCA) using "vegan" package to confirm that we were able to test the biodiversity of birds across Europe and North Africa (Fig. A2 and Table A2, Online Resource 5). All figures were produced using "ggplot2" (Wickham 2016).

3. Results

3.1 Taxonomic diversity

There were no evident changes in species richness or Shannon diversity in relation to the first axis representing management intensity (p>0.05). Both species richness and diversity decreased towards more densely treed and less heterogeneous areas (second axis representing management intensity), but neither trend was significant (p>0.05) (Fig. A3 and Table A3, Online Resource 5).

3.2 Functional diversity

Functional diversity showed a significant response to management, generally decreasing towards lower management intensity. FRic showed a nearly-significant decrease in relation to PCA axis1 (p=0.08), and thus towards areas with less management, where shrub cover and shrub height are higher (Fig. 2a). Fdis (p<0.001; R^2=-0.29) and FEve (p≤0.01, R2=-0.21) also decreased towards shrub-dominated and less heterogeneous areas (Figs. 2b and 2c), and in both cases the decrease was significant. No significant associations were detected between FD indices and the second PCA axis (p>0.05). All diversity data is available in Table A4, Online Resource 5.

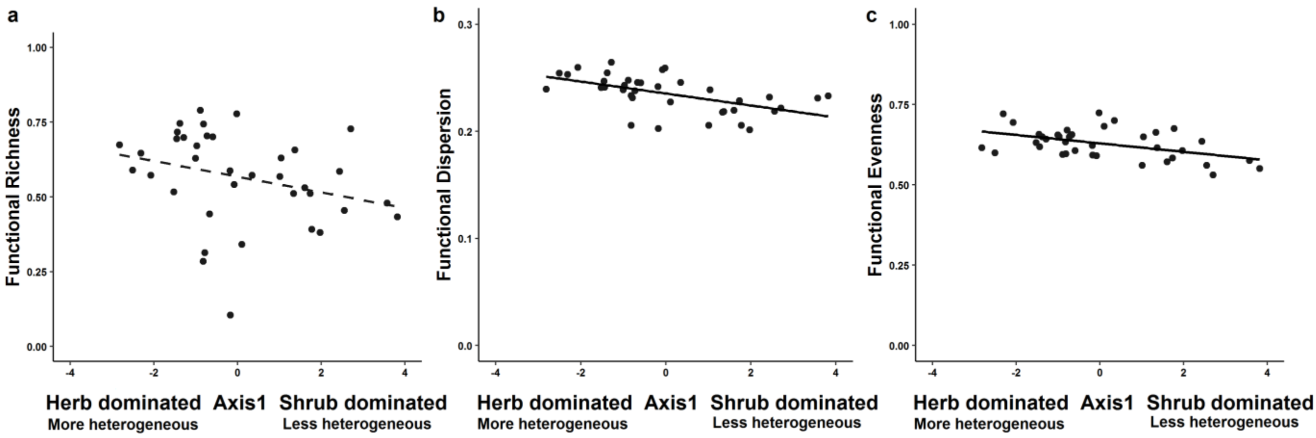

Fig. 2 Relation of bird functional diversity to habitat structure, represented by the first PCA axis. All variables decrease towards shrub dominated, less managed areas, but the trend is significant

only in (b) and (c), represented by solid trend lines. See Table A4, Online Resource 5 for test statistics of linear models.

3.3 Functional composition

We observed significant variations in feeding guild, foraging strata, nest type and habitat use traits of birds along the management gradient represented by the first PCA axis (Table A5, Online Resource 5). CWM of grassland species ($p<0.001$; R^2=-0.56) and generalists ($p\leq0.05$; R^2=-0.08) significantly decrease towards shrub dominated areas, while forest species ($p<0.001$; R^2=0.46) show the opposite trend. However, it should be noted that forest species are still well represented in more open and heterogeneous areas, where they compose approximately half of the observed bird communities, whereas grassland specialist species are often absent in shrub dominated areas (Fig. 3a).

CWM of granivores ($p\leq0.05$; R^2=-0.11) decreases significantly towards less managed, shrub-dominated areas. However, the CWM of omnivore and insectivore species ($p>0.05$) did not vary significantly in relation to any of the habitat variables, indicating their relative abundance remains constant independently of habitat structure (Fig. 3b). The relative abundance of ground-foragers ($p<0.001$; R^2=-0.39) also decreases with higher shrub cover in areas tending towards abandonment, while species foraging in the canopy ($p<0.001$; R^2=0.34), midhigh ($p\leq0.01$; R^2=0.20) and understory ($p<0.001$; R^2=0.35) benefit from the abundant woody vegetation available in these areas (Fig. 3c). Closed-ground nesters ($p\leq0.05$; R^2=-0.21) are better represented in open and heterogeneous areas maintained by active human management. On the other hand, closed-arboreal ($p\leq0.01$; R^2=0.15) and open-arboreal ($p\leq0.05$; R^2=0.12) nesting birds are more prevalent in less managed areas with higher shrub cover and tree density (Fig. 3d).

Only wing aspect ratio ($p\leq0.05$; R^2=-0.08) decreased with intensive shrub management, as suggested by the significant negative relation to the second PCA axis (Fig. A4, Online Resource 5).

We did not observe significant variations in body mass, tree/cavity and bare ground nesting types in relation to habitat variables (Table A5, Online Resource 5).

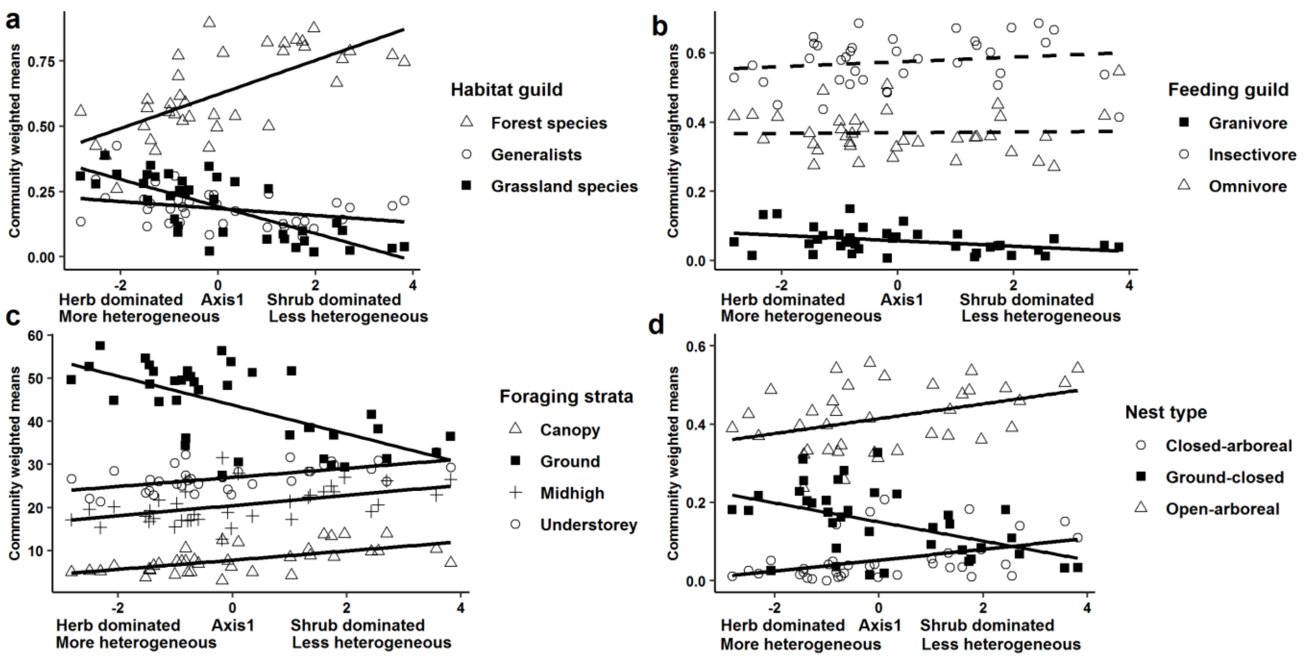

Fig. 3 Community weighted means (CWM) of functional traits across the management gradient. CWM of generalists and grassland species (a) granivores (b) ground-foragers (c) closed-ground nesters (d) decreases towards shrub dominated, less managed areas, while forest species (a), canopy and understory foragers (c) and arboreal nesters (d) benefit from shrublands. Solid and dashed lines indicate significant ($p \leq 0.05$) and non-significant trends, respectively. See Table A5, Online Resource 5 for test statistics of linear models.

4. Discussion

4.1 Land abandonment leads to decreases in bird functional diversity, but not in taxonomic diversity

Our results show that changes in vegetation structure and habitat heterogeneity linked to land abandonment influence trait-level diversity of birds during the breeding season, but do not influence taxonomic diversity. Neither species richness nor Shannon diversity metrics responded to changes in habitat structure, indicating the presence of diverse species assemblages across the management gradient (Fig. A3, Table A3, Online Resource 5). However, we found a significant decline of functional dispersion and evenness toward less managed areas (Fig. 2), suggesting that trait assemblages are more similar and less evenly distributed in wood-pastures within areas undergoing active management (Hillebrand et al. 2008; Crowder et al. 2010). Studies report contrasting trends in species and trait-level responses to various management strategies, suggesting the need to explore different dimensions of biodiversity to understand the complex relation of species to the ecosystem (Devictor et al. 2010). Our results support this view and suggest more pronounced trait-level responses to changes in wood-pasture structure than those observed at the species-level, mostly due to the loss of traits of grassland birds (Fig. 3a). Variations in niche structure due to different management strategies are likely to explain the observed patterns, which can benefit or impair species with specific traits without necessarily leading to changes in taxonomic diversity (Gagic et al. 2015).

Land abandonment in wood-pastures is often characterised by a reduction in grazing and the absence of activities commonly used to improve grazing potential, namely shrub removal, resulting in higher tree and shrub densities, denser canopies and a decrease in habitat heterogeneity (Castro and Freitas 2009; Oldén et al. 2017). Grassland species usually depend on open mosaics of habitats to feed and nest (Reino et al. 2010), therefore the presence of denser and taller woody vegetation is likely to reduce the availability of suitable conditions for these species (Sirami et al. 2007; Spitzer et al. 2008). Our results suggest this is indeed the case in wood-pastures as the relative abundance of grassland species decreased towards areas with denser and taller shrubby vegetation (Fig. 3a). Grassland bird populations have suffered severe declines in recent decades all across Europe mostly because of land-use intensification (Butler et al. 2010), but our findings underline land abandonment may be another factor negatively affecting this guild. Traits such as ground nesting, ground feeding and granivory are often available only in open areas, also decreased towards abandoned areas (Fig. 3). These changes are likely due to the presence of dense shrubby vegetation in these areas, which can substantially restrict seed availability, predator detectability and the availability of suitable ground foraging sites for these species (Vickery and Arlettaz 2012).

In contrast, our results show forest species may benefit from land abandonment (Fig. 3a) and similar results observed in wood-pastures across Europe (Sirami et al. 2009; Nikolov et al. 2011; Jakobsson et al. 2018). Dense shrublands are known to be suitable for forest species such as *Erithacus rubecula*, *Sylvia atricapilla* and *Troglodytes troglodytes* by providing feeding resources and reducing predation (Santana et al. 2012). Furthermore, the availability of nesting sites for arboreal nesters is likely to increase in densely wooded areas, as our results present (Fig. 3). We also observed significant differences in birds linked to different foraging strata (Fig. 3), which is informative of the way birds use the habitat under different management strategies (Martin and Possingham 2005). The abundance of understory and canopy foragers increases whereas ground foragers decrease in less managed areas, suggesting that land abandonment leads to changes in different foraging strata use.

There may be important consequences to wood-pasture ecosystem dynamics related to vertical shift of birds towards higher foraging strata in less managed areas. For example, many oak pest species spend at least part of their life-cycle on or under the ground (Ceia and Ramos 2016). Ground foraging birds may thus play an important role controlling these pests, but this role may be limited in areas with dense ground vegetation, as our results further suggest.

We also observed that bird assemblages in more homogeneous areas with higher tree density and less shrubs tend to feature more birds with a lower wing aspect ratio (Fig. A4, Online Resource

5). Lower wing aspect ratio represent shorter and more rounded wings allowing for better manoeuvrability in densely treed habitats (Vanhooydonck et al. 2009) but are less suited for longer distance flights.

4.2 Active management maintaining habitat heterogeneity supports functionally diverse bird communities in wood-pastures

Our results provide evidence for the important role of management in maintaining bird functional diversity in wood-pastures. Extensive grazing acts to maintain the characteristic habitat heterogeneity of wood-pastures which is crucial to provide diverse feeding and nesting resources for birds (Tews et al. 2004; Leal et al. 2019) particularly during the breeding season (Mag and Ódor 2015). Grassland species are especially dependent on resources that are only available in more open and heterogeneous areas, which are usually sustained by extensive grazing (Reino et al. 2010). Generalists also seem to increase with active management, whereas forest species dominate the assemblage in the denser habitats that results from land abandonment. However, we underline that forest species were also present in open managed areas, where they comprised approximately half of the bird community, whereas grassland species are often absent in densely vegetated areas (Fig. 3a). This result indicates that by maintaining habitat heterogeneity, actively managed areas can provide a wide range of niches, inclusively for most forest species.

While active management seems necessary to maintain heterogeneous wood-pasture landscapes, the intensity of management also plays a key role. There is evidence that in highly exploited systems, reducing management intensity level can be advantageous providing more suitable and connected habitats for species narrower niche requirements (Queiroz et al. 2014). On the other hand, studies focusing on multiple species responses to land abandonment also report the potential threats of this change in land-use types to the overall biodiversity value of managed habitats (Horák et al. 2018a). Specifically, land abandonment may ultimately lead to the functional homogenization of biological communities in Mediterranean habitats (Clavero and Brotons 2010) due to a loss of habitat heterogeneity, as our results also indicate.

It is obvious that both habitat intensification and abandonment can have adverse consequences for the biodiversity of wood-pastures, whose preservation depends on the maintenance of habitat heterogeneity emerging from multi-purpose management strategies (Mönkkönen et al. 2014; Roellig et al. 2016). As more traditional management strategies struggle to maintain the economic sustainability of wood-pastures, the challenge for the future is to find simple and inexpensive management strategies that conciliate economic and natural values in wood-pastures.

Ultimately, our results propose that maintaining active management may lead to higher response trait diversity of birds in wood-pastures. Lastly, we should underline that the traits we analysed are both "response and effect traits", implying that many of the trait-level changes observed may also reflect greater effect on the ecosystem services (de Bello et al. 2010; Torralba et al. 2016).

5. Conclusions

We show substantial shifts in bird assemblage functional diversity and composition, in response to vegetation structure and habitat heterogeneity changes associated with land abandonment in wood-pastures. These changes seem to be unfavourable for grassland and generalist species with life-history traits such as ground nesting, granivory and ground feeding, ultimately leading to loss of bird functional diversity and potentially hampering the range of ecosystem services that birds can provide. In many regions, wood-pastures are undergoing a transformation from multi-functional heterogeneous systems to more homogeneous habitats, due to a reduction of management resulting from multiple socio-economic pressures (Hartel et al. 2015). The abandonment of traditional management, and the subsequent encroachment of woody vegetation, are increasingly threatening the biodiversity of many European habitats (Queiroz et al. 2014). Balancing the natural and economic values of human-modified habitats is one of the main challenges in improving conservation efforts (Graves et al. 2007; Landis 2017) and our results suggest that maintaining non-intensive, active management may be a sustainable answer to this challenge in wood-pastures.

Declarations

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Conflicts of interest

The authors have no relevant financial or non-financial interests to disclose.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

All data generated or analysed during this study is included in Supplementary Information files (Online Resources 1 and 2).

Code availability

Not applicable.

Authors' contributions

Duygu P. Oksuz: Conceptualization, Data Curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review&editing.

Jorge M. Palmeirim: Conceptualization, Methodology, Supervision, Funding acquisition, Writing-review&editing.

Ricardo A. Correia: Conceptualization, Data Curation, Investigation, Methodology, Funding acquisition, Supervision, Writing-review&editing.

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