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# Role of the Mediterranean Sea in differentiating European and North African woodland bird assemblages

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Abstract: The Mediterranean Sea has separated the sclerophyllous forests of southern Europe and northern Africa for millions of years, but its role structuring forest bird assemblages remains unclear. To address this issue we sampled bird assemblages in cork oak woodlands located north and south of the Strait of Gibraltar and compared abundance, diversity, and species and guild assemblage structure between regions. Abundance and diversity patterns were remarkably similar, but dissimilarity analyses of species and guild composition revealed differences in bird assemblage structure between regions. Differences are partly attributable to the effect of the Mediterranean as barrier to the dispersal of forest birds; a few species were unable to colonize North Africa, and many that colonized it remained in sufficient isolation to evolve into distinct taxa. In addition to this divergence of biogeographic genesis, assemblages also differ because in North African cork oak woodlands forest and insectivorous specialist species are less abundant. This dissimilarity could be due to the effect of different exploitation levels present in each region. Managed cork oak woodlands are widespread in the Western Mediterranean, and are valuable because they conciliate economic exploitation with high biodiversity. In North Africa these woodlands are of greater conservation concern because they harbour endemic bird species that give its assemblage a distinct character, cover a smaller area, and are currently under greater pressure from overexploitation. These results highlight the importance to implement management practices that increase resilience and maintain biodiversity value throughout the range of cork oak woodlands.

Nomenclature: Gill and Donsker (2015).

Abbreviations: GLM-Generalized Linar Model, LR-Log-likelihood Ratio.

### Introduction

The Mediterranean Basin is considered a hot-spot of biodiversity (Myers et al. 2000), which is to a great extent a consequence of the topo-geographical complexity of the region (Blondel et al. 2010). The Mediterranean Sea is its most evident geographic feature, physically separating the terrestrial ecosystems of southern Europe and northern Africa. The last time this separation was interrupted in the Western Mediterranean was over five million years ago, when geological forces temporarily closed the Strait of Gibraltar, causing a partial desiccation of the landlocked sea (Duggen et al. 2003).

The role of the Mediterranean Sea as a barrier to gene flow within species is relatively well studied (e.g., Broderic et al. 2003, García-Mudarra et al. 2009, Pons et al. 2011, Husemann et al. 2014), but its effects on the structure of species assemblages across the region remain somewhat unexplored. Indeed, such an extensive barrier to dispersal of biota may cause the differentiation of assemblages by limiting

colonization across the barrier, and by facilitating speciation of isolated populations. Several studies confirmed speciation processes across the Strait of Gibraltar in multiple taxa, although the frequency of this phenomenon is greatly dependent on the dispersal abilities of each taxon; flying species, and those that tolerate salt water, tend to show lower levels of differentiation across the Strait (Habel et al. 2009). Existing information is still insufficient to make broad generalizations about the level of permeability of the Strait for birds, but evidence indicates that it is lower in forest-adapted birds than in arid-adapted species (Pons et al. 2011). Evidence that some forest-adapted species have differentiated populations in Iberia and North Africa is growing (Saetre et al. 2001, Broderick et al. 2003), reinforcing the need to evaluate the role of the Mediterranean Sea on regional bird assemblages.

The structure of species assemblages on the two sides of the Mediterranean may not differ solely due to its natural role as a barrier to dispersal, but also because it separates two highly contrasting socio-economic realities. These contrasts translate into different land use practices, which are known

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to have a marked influence on biological communities and ecological processes across the region (Blondel et al. 2010).

Large areas of the Western Mediterranean basin are dominated by cork oak (Ouercus suber) woodlands, usually managed as an agro-silvo-pastoral system known as Montado in Portugal and Dehesa in Spain. This system resulted mostly from the transformation of original cork oak forests through a long history of low intensity management (Díaz et al. 1997) and harbours some of the richest bird assemblages in the Mediterranean region, both in Europe and in North Africa. The value of managed cork oak woodlands for bird diversity is widely acknowledged and many were classified as Important Bird Areas in both Europe and North Africa (Heath et al. 2000, Fishpool and Evans 2001). Their overall high importance for biodiversity also resulted in their classification as High Nature Value Farmland (Hoogeveen et al. 2004) and in the inclusion on the list of habitats to protect under the European Habitats Directive (92/43/EEC).

While the overall structure of cork oak woodlands is generally similar between continents, their bird assemblages may differ not only because of the separation by the Mediterranean but also due to contrasts in exploitation that result from different socioeconomic realities (Bugalho et al. 2011). Cork removal is usually their main economic activity, but grazing, wood and acorn collection, hunting, and recreation are also common. Cork oak woodland abandonment is an increasing problem in parts of Iberia but most woodlands are sustainably exploited, which is important for the maintenance of high biodiversity levels (Bugalho et al. 2011). In contrast, habitat overexploitation is presently common in many Northern African woodlands, which may affect soil quality, vegetation structure and local biodiversity. For these reasons, cork oak woodlands are particularly well suited to investigate the process of differentiation of bird assemblages, separating the role of the Mediterranean Sea as a barrier for forest birds and that of human induced factors.

The general aim of this study is to contribute to the understanding of the barrier role of the Mediterranean Sea in the structuring of biological communities, by evaluating its relevance shaping woodland birds assemblages. In addition, we quantified the relative importance of this role and that of woodland exploitation and management. To achieve these objectives we compared the bird assemblages of North African and Iberian cork oak woodlands, testing for differences in (i) assemblage structure (species richness and abundance) and (ii) assemblage composition (both species and guild-assemblages). The results of these comparisons are discussed in the light of the complex bio-geographical history of the Mediterranean Basin (Blondel et al. 2010) and of the current threats to cork oak woodlands (Berrahmouni et al. 2009).

### Material and methods

Study area

To control for the fact that many bird species tend to increase their abundance with distance to the Strait of Gibraltar (Tellería and Santos 1993), all study sites are located within 100 km of the strait (Fig. 1). The region has a complex topography and a Mediterranean climate, with mild winters and dry warm summers. Annual temperatures average around 15 °C and annual precipitation is usually over 600 mm (Ojeda et al. 1996). The indigenous vegetation of the region is typically Mediterranean, and woodlands are common and in general dominated by the evergreen cork oak (*Quercus suber*), although holm oak (*Q. rotundifolia*), Algerian oak (*Q. canarensis*) and Pyrenean oak (*Q. pyrenaica*) are also locally abundant (Marañón et al. 1999, Ajbilou et al. 2006). Despite this fact, local patches of farmland and/or pastures can also be found in the region.

We sampled bird assemblages in a total of seven cork oak woodlands, four in Iberia and three in North Africa (see cen-

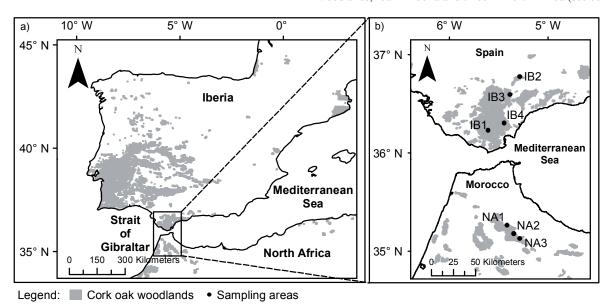


Figure 1. Regional (a) and local (b) distribution of cork oak woodland (shaded areas) and location of the sampled areas (dots).

tral point coordinates in Supplementary Material Appendix 1). Woodlands were selected based on road and land accessibility. The main source of revenue of all these exploited woodlands is cork extraction, but recently harvested areas were avoided since this practice can temporarily affect bird assemblages (Leal et al. 2011a). In Iberia study areas were mostly private, whereas in North Africa they were state owned and had open access. Vegetation structure was roughly similar in all areas, with tree density averaging around 60 trees/ha. Shrubs were usually less than 1m high and generally covered more than 60% of the ground surface. Grass cover varied with grazing levels, and was particularly sparse and short in North African areas.

### Bird sampling

We sampled bird assemblages using five-minute bird point counts (Sutherland et al. 2004, Bibby et al. 2005) during the spring of 2011. The same observer sampled fifteen counting stations in each of the seven sampled woodlands. Counting stations were separated by at least 200 m and were located 100 m or more from woodland edges. All stations were sampled during the early and late halves of the breeding season (once between 1 April and 15 May; once between 16 May and 20 June), to account for the presence of migratory species. This resulted in a total of 210 point counts, which were carried out during periods of peak activity and avoiding rainy or windy days (Sutherland et al. 2004). All birds detected, visually or acoustically, within 100 m from the observer were recorded and their distance was estimated. Over-flying birds and those detected more than 100 m from the observer were recorded, but not included in the analysis.

# Data analysis

Bird species were classified into habitat, feeding and nesting specialization guilds. Habitat guild classification includes forest and farmland specialists and species associated with other habitats, based on the European Bird Census Council habitat classification for Mediterranean countries (EBCC 2010). Feeding guild classification includes insectivore, granivore and generalist species based on Cramp and Simmons (2006). Nesting specialization guilds included tree nesting, undergrowth nesting (includes species nesting on the ground) and generalist species, also based on Cramp and Simmons (2006). The number of birds of each species detected in each of the fifteen point counts was summed for each area and visit. For each species, the total number of birds detected was then compared between visits and the maximum number detected in either of the two visits was considered as the total abundance of that species in the area. This number represents the minimum number of birds present at that location (Bibby et al. 2005) and was further considered for analysis. No compensation for detectability was used to estimate abundance because sample size was small for many species, but this should not affect our comparisons, as any biases due to detectability are likely to be similar in both regions.

We estimated species richness with Coleman individualbased rarefaction curves computed using EstimateS v8.2 (Colwell 2009). These curves allow for richness estimation while controlling for confounding effects of bird densities and sampling effort (Gotelli and Graves 1996). We also calculated mean bird abundance and Shannon and Equitability indexes for each region, and compared them using Student's *t*-tests.

The structure of the assemblages was compared using abundance data, to obtain more meaningful estimates of similarity; incidence-based similarity comparisons treat rare and abundant species equally and thus tend to oversimplify relationships between assemblages (Gotelli and Chao 2013). Prior to the analyses, we applied the Hellinger transformation for abundance data (standardized per site and square-root transformed), and calculated a dissimilarity matrix with distances between the seven sampling areas (Borcard et al. 2011), using the vegan package implemented in R (R Development Core Team 2011). However, due to recent criticism of distancebased multivariate analysis (Warton et al. 2012), we tested for differences in the structure of bird species and guild assemblages between regions using multivariate generalized linear models (GLM) for high-dimensional data, available through the mvabund R package. We fitted a multivariate GLM with negative binomial error distribution (following Warton et al. 2012) on the untransformed abundance data and used a multivariate ANOVA with log-likelihood ratio (ANOVA LR) to test for differences between the assemblages of the two regions and to assess the contribution of individual species for these differences. Finally, and based on the checklists of birds for Spain and Morocco (Lepage 2013a,b), we classified the species in two distribution groups: restricted (species restricted to either North Africa or Europe) or widespread (species present in both regions). We assessed the contribution of each of these groups to the total difference between assemblages (the sum of the contributions of all species in the group). Differences due to restricted species are likely to be a consequence of the barrier effect of the Mediterranean, whereas those due to widespread species are presumably the result of local factors, including human-induced factors. A list of the recorded species indicating their habitat, feeding and nesting specialization guild and geographic distribution classification can be found in Supplementary Material (Appendix 2).

# Results

Species richness and abundance

The 210 bird point counts resulted in the detection of a total of 1412 individuals of 46 species (Fig. 2). The five most abundant species (*Erithacus rubecula*, *Fringilla coelebs*, *Parus major*, *Sylvia melanocephala* and *Turdus merula*) represented approximately 45% of the individuals sampled, whereas 30% of the species sampled were represented by five or fewer birds. The majority of individuals belonged to forest specialist species (64%) followed by generalist species (23%). Species in the shrub and farmland guilds represented

Table 1. Key parameters of the bird assemblages of Iberian and North African cork oak woodlands.

Region	Na	Abundanceb	Species richness <sup>c</sup>	Shannon index	Equitability index
Iberia	4	4.46±0.83	27.0±5.1	2.86±0.18	0.77±0.05
North Africa	3	4.03±0.24	25.3±1.5	$2.76 \pm 0.08$	$0.77 \pm 0.02$

a Number of sites sampled

**Table 2.** Average dissimilarity scores based on the Hellinger dissimilarity index for species and guild assemblages, within and between regions.

Region	Dissimilarity index				
	Species	Habitat guilds	Feeding guilds	Nesting guilds	
Within Iberia	0.51	0.12	0.10	0.13	
Within North Africa	0.49	0.14	0.11	0.11	
Between Iberia-North Africa	0.74	0.17	0.15	0.12	

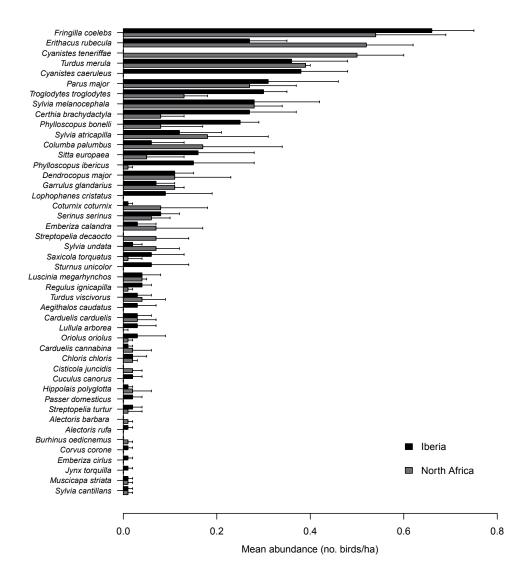
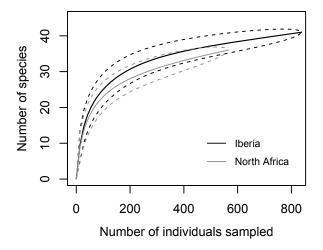


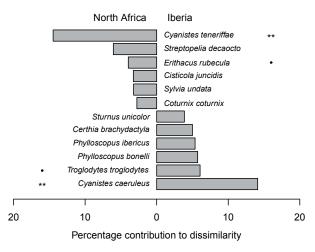
Figure 2. Mean abundance and 95% confidence intervals of each species registered in North African and Iberian cork oak woodlands. Species are ordered according to their maximum abundance observed in both regions.

<sup>&</sup>lt;sup>b</sup> Mean and 95% confidence interval of the total number of birds per hectare

<sup>&</sup>lt;sup>c</sup> Mean and 95% confidence interval of the number of species per sampled site



**Figure 3.** Individual based rarefaction curves of species richness for areas north and south of the Strait of Gibraltar. Dotted lines delimit the 95% confidence envelopes.



**Figure 4.** Species making the highest contributions (>2.5%) to assemblage dissimilarities between regions. Species with significant (\*\* P<0.01) and nearly significant (\* P<0.10) differences between regions are highlighted in the figure.

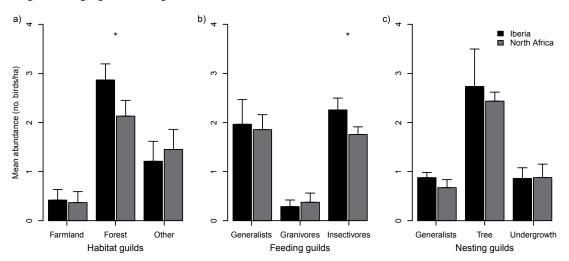
just eight and five percent of the total individuals, respectively.

Average bird abundance (t=0.98, df=3.7, P=0.39) and number of species detected per site (t=0.52, df=3.1, P=0.64) did not differ significantly between regions (Table 1). The Shannon diversity index (t=1.12, df=3.9, P=0.33) and the Equitability index (t=0.10, df=3.9, P=0.92), were not distinct between regions either. Individual based rarefaction curves indicate that species richness is similar in both regions, even when taking into account their unequal sampling effort, reinforcing the similarity between regions (Fig. 3).

## Species composition

The results of the point counts (Fig. 2) show that there is much in common between the species assemblages of cork oak woodlands of southern Iberia and northern Africa. This is evident both in the species present and in their abundance. Nonetheless, the dissimilarity analysis of species assemblages (Table 2) shows that the sampling sites were more dissimilar between regions (0.74) than within them (0.51 and 0.49 for African and Iberian areas, respectively). These results suggest a difference between regions, and this was confirmed by the significant results obtained with multivariate GLM analysis (ANOVA LR; *SD*=149.6, df=5, *P*=0.005).

In light of these results, we assessed the contribution of individual species to the difference between the studied assemblages in Iberia and northern Africa (Fig. 4). Only two species made a statistically significant contribution to this difference: *Cyanistes caeruleus* (ANOVA LR test; *SD*=21.1, df=5, *P*<0.01), in Europe, and *C. teneriffae* (ANOVA LR test; *SD*=21.7, df=5, *P*<0.01), in North Africa. Two other species, although common in both regions, had a nearly significant contribution: *E. rubecula* (ANOVA LR test; *SD*=1.1, df=5, *P*=0.09) and *Troglodytes troglodytes* (ANOVA LR test; *SD*=1.1, df=5, *P*=0.09). Species restricted to either Europe or North Africa were responsible for 33% of the total difference, while those present in both regions explained the remaining 67%.



**Figure 5.** Mean abundance and 95% confidence intervals of habitat (a), feeding, (b) and nesting (c) guilds for both studied regions. Asterisks indicate significant differences between regions (P<0.05).

## Guild assemblage

Dissimilarity analysis for guild assemblage also revealed that sampling sites were less dissimilar within regions than between them for habitat and feeding guilds (Table 2). The same was not true for nesting guilds, which showed negligible differences on dissimilarity values within and between regions. Multivariate GLM analysis on guild structure between regions reflected this situation and revealed significant differences between regions in terms of habitat (ANOVA LR; Dev=8.2, df=5, P=0.03) and feeding guilds (ANOVA LR; Dev=8.3, df=5, P=0.03), but not for nesting guilds (ANOVA LR; Dev=4.8, df=5, P=0.28).

Forest species were the only habitat guild showing significant differences (ANOVA LR test; *Dev*=7.3, df=5, *P*=0.02) in abundance between regions according to ANOVA log-likelihood ratio tests. For feeding guilds, ANOVA log-likelihood ratio tests revealed significant differences in abundance between Iberia and North Africa for insectivorous species only (ANOVA LR test; *Dev*=7.4, df=5, *P*=0.02). No significant differences were found in the abundance of any of the analysed nesting guilds between regions.

### Discussion

How different are the bird assemblages of European and African cork oak woodlands?

Our study found that bird assemblages of Iberian and North African cork oak woodlands are structurally quite similar. Overall bird abundance is similar, and so is the species richness of the assemblages (Table 1). Values for both parameters are in line with those described for other Mediterranean oak woodlands (Telleria 2001). The total number of species observed in the counts was higher in Iberia but the rarefaction analysis indicates that this is due to a greater sampling effort. In fact, most species observed only at Iberian sites are also occasionally present in the North African cork oak woodlands that we sampled (Cherkaoui et al. 2009 and personal observations), but are not abundant and were not detected during the point counts for stochastic reasons.

In spite of this resemblance in assemblage structure, the species-level abundance analysis revealed a statistically significant difference between the species and guild assemblage composition of the two regions. The species that contribute most to that difference, *Cyanistes caeruleus* (Iberia) and *C. teneriffae* (North Africa) are phenotypically so similar that until recently were considered conspecific (Salzburger et al. 2002). They presumably occupy the same niche in both regions and are thus functionally equivalent. An analogous situation occurs with the pair *Alectoris rufa* (Iberia) and *A. barbara* (North Africa). Differences due to such species pairs are biogeographically relevant, as discussed in the next section, but do not correspond to ecologic structural differences between the assemblages.

It is thus likely that the similarity of the two assemblages is explained by a combination of analogous ecological conditions, permeability of the Mediterranean to dispersal, and a long common history. The bird fauna of cork oak woodlands essentially mirrors that of natural Mediterranean woodlands, which is known to harbour mostly the same species in Europe and North Africa (Blondel 1995). Palaeoecological evidence indicates that during the Pliocene and Pleistocene parts of southern Europe and North Africa had comparable climatic and ecological conditions, leading to similarities in the faunas of the two regions (Husemann et al. 2014). Comparable conditions persisted even during the Pleistocene glacial periods and in fact southern Iberia and the adjacent areas of North Africa have been classically merged in the same glacial refuge, the Atlantic-Mediterranean centre (De Lattin 1949). In the case of birds, as in that of other flying organisms (Habel et al. 2009), the Mediterranean remained a relatively permeable barrier, which partly prevented local differentiation processes and facilitated the homogenisation of the assemblages during this period.

However, the two assemblages also differed in their guild structure, mostly because of forest and insectivorous specialist species that are present in both regions but appear in greater abundance in Iberia when compared to northern Africa. The role of the Mediterranean Sea in the differences observed between regions, both in terms of species and guild composition, is discussed in the next section.

How important is the barrier role of the Mediterranean in the differentiation of the two assemblages?

The Mediterranean has been a barrier for dispersal of terrestrial biota for over five million years. Studies done with different animal groups found that for most of them this barrier has been of major biogeographic importance (Husemann et al. 2014). Our comparison between bird assemblages of the same habitat on opposite sides of the Mediterranean contributes to the understanding of its potential role structuring forest bird communities.

A major barrier to dispersal can differentiate assemblages by preventing the exchange of species through colonization, and by promoting speciation through the minimization of gene flow. There is evidence that both mechanisms contributed to some extent to the observed differentiation between North African and European cork oak woodland bird assemblages. Two of the species detected at our European study sites, Lophophanes cristatus and Aegithalos caudatus, are present all the way to the northern shores of the Strait of Gibraltar but are absent from North Africa. The lack of information regarding their distribution during the glacial periods makes it difficult to determine if these species were ever present in Northern Africa. Nonetheless, their current absence from the region indicates that the open ocean at the Strait has at some point prevented them from colonizing suitable habitats in North Africa. Nonetheless, this impediment of colonization was quite rare, and species of Eurasian origin tend to dominate the forest breeding bird assemblages of North Africa (Blondel et al. 2010).

Although virtually all forest bird species were able to cross the Mediterranean and colonize North Africa, it constitutes a sufficient barrier to minimize gene flow and allow differentiation. In some cases this differentiation has been sufficiently strong to result in full speciation, and a relevant proportion of the difference between our studied assemblages is due to such differentiation. An example of this speciation due to the barrier effect of the Mediterranean is the pair C. caeruleus and C. teneriffae (Salzburger et al. 2002). Other examples include North African endemics that also occasionally inhabit cork oak woodlands, such as Picus vaillantii that evolved from P. viridis (Pons et al. 2011), and Ficedula speculigera that evolved from F. hypoleuca (Saetre et al. 2001). Differentiation also occurred in several other woodland birds, which are represented in North Africa by endemic subspecies, as in the case of Strix aluco mauritanica (Brito 2005).

While it seems clear that the Mediterranean is more permeable to birds than to most other groups of animals so far studied (Husemann et al. 2014), this barrier could also have an indirect impact on bird assemblages by acting on the distribution of species that are important for birds, as either resources or predators. For example, tree diversity is lower on the southern side of the Strait, and part of that difference has been attributed to historical biogeographic processes (Rodríguez-Sánchez et al. 2008). Such ecological differences between the north and south of the Strait could change the suitability of the habitat for some bird species, and thus influence their patterns of relative abundance. However, despite significant, the barrier effect of the Mediterranean does not explain most of the observed dissimilarity in species and guild assemblage at our study sites. In fact, restricted range species, i.e. those only present in either Iberia or North Africa, account for just a third of that dissimilarity. The remaining dissimilarity reflects differences in the abundance of species that are present in both regions. These are most likely due to local ecological factors (e.g., management practices, habitat composition and diversity) than to historical regional processes, particularly as we cannot exclude that some of the differences may be due to dissimilarities in the surrounding habitat matrix (Leal et al. 2011b).

## Implications for conservation

Although North African cork oak woodlands harbour a bird assemblage that is quite similar to that of the same habitat in Europe, we found that its isolation by the Mediterranean Sea resulted in a distinct character that should be preserved. The presence of several North African endemics with a small global range (*C. teneriffae*, *P. vaillantii*, *F. speculigera*, *Sitta ledanti*, *Phoenicurus moussieri*) is an important part of this distinctiveness and conservation value. In addition, several of those endemic species (and subspecies) have their closest relatives across the Mediterranean, which indicates that these woodlands are hosting ongoing historical-evolutionary processes that should be maintained.

Cork oak woodlands represent a particularly good habitat to protect birds and other wildlife because its economic exploitation, most often based on cork extraction and grazing,

is usually compatible with the maintenance of high levels of biodiversity (Plieninger and Wildebrand 2001). However, in spite of its high natural value, the area covered by cork and other oak woodlands in North Africa is much smaller than that in Europe and is under greater human pressure. For example, overgrazing and over-collection of wood are more common in North African woodlands (Marañón et al. 1999, Bugalho et al. 2009, Bugalho et al. 2011), partly due to open public access. When intensive, such practices are known to alter habitat structure and resource availability for birds (Godinho and Rabaça 2011, Leal et al. 2013). In traditionally managed areas, sustainable exploitation is usually necessary to maintain high biodiversity levels (Bugalho et al. 2011), but overexploitation is detrimental and is already affecting birds (Cherkaoui et al. 2009) and plants (Marañón et al. 1999) in North Africa. Other taxa, like mammals (Rosalino et al. 2011) and insects (Silva et al. 2009), are also likely to be affected. We found that most of the difference in the cork oak bird assemblages of Europe and North Africa reflects the lower abundance of forest and insectivorous specialist species in the latter region. This may be a result of overexploitation and indicates a reduction of the efficiency of this economically valuable habitat as a surrogate for the conservation of natural Mediterranean forests and associated biodiversity.

Furthermore, the range of the cork oak woodlands is under increasing pressure by climate change, and there is evidence that this phenomenon is already affecting cork oaks and other Mediterranean trees (Carnicier et al 2010). While this is a major problem throughout the region, it is likely to be particularly serious in North Africa for two reasons. First, because North Africa is closer to the aridity limit of the cork oak, and woodlands in this region are thus presumably more vulnerable to further intensification of aridity. Second, because while in Europe the loss of climatically suitable range of the cork oak may be partly compensated by a northward range migration, this is not a possibility in North Africa.

In conclusion, we found that bird communities of Cork oak woodlands on both sides of the Mediterranean are equally rich and share many similarities. However, there are species unique to either side, resulting in a differentiation due to natural historical processes that make the preservation of the two assemblages very important. Overexploitation seems to be affecting the structure of cork oak woodland bird assemblages, especially in North Africa. In this region the situation is particularly worrisome because its cork oak woodlands are less extensive than in Europe and they harbour a bird assemblage rich in endemic species and subspecies. Throughout their range cork oak woodlands remain a valuable surrogate for the conservation of the birds and other biodiversity associated to the now very scarce natural Mediterranean woodlands, but conservation measures and better management are needed to increase resilience and maintain their value, especially in North Africa.

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# Appendix 1

Geographic coordinates of each sampling area provided as a Google Earth (.kmz) file.

# Appendix 2

Summary table of the species detected in each area and their abundances in Iberian and North African cork oak woodlands.

The files may be downloaded from www.akademiai.com