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Environmental determinants of seasonal changes in bird diversity of Mediterranean oakwoods

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Abstract The strong season-to-season variation (seasonality) in abiotic factors and productivity shape the changing patterns of species distribution and diversity throughout the year in temperate ecosystems. However, the determinants of seasonal changes within animal communities have rarely been explored, and the prognosis of community variation typically relies on identifying simple factors (e.g., mean temperature) that are assumed to have a constant effect throughout the year. Here we analyze the competing and changing roles of biotic (vegetation structure and phenology) and abiotic (temperature and elevation) factors in determining the richness and nestedness of montane Mediterranean oakwoods (central Spain) bird species in winter and spring. In winter, the most energy-demanding period, birds prefer mature forests with higher nocturnal temperatures where they can minimize thermoregulation costs during the long winter nights. In spring, which is the breeding season, spatial variation of species richness and nestedness is more deterministic than in winter. Breeding birds prefer lower forests with cooler temperatures at midday (presumably to avoid summer overheating stress), less unpredictable weather, and where trees develop leaves earlier (suggesting that birds, particularly those that prey on folivorous insects, would be able to breed early in the season). Thus, although both biotic and abiotic factors take part in the assemblage of local communities, the intervening specific components vary between seasons. For example, temperature—the factor most widely used to forecast future community changes—had opposite effects in winter than in spring.

These results highlight the importance of fine-grained scale studies in accounting for temporal variation to understand both current and future regional biodiversity patterns.

Keywords Habitat characteristics · Nestedness · Species richness · Temperature · Winter

Introduction

At northern mid and high latitudes, a strong seasonality in abiotic conditions and productivity imposes widely different ecological scenarios throughout the year on the communities living in them (Breckle 2002). Seasons impose contrasting demands on animal species, which must respond with behavioral and physiological adaptations, including shifting resource use or migration to other geographical areas with tolerable or more adequate conditions (Wagner 1981; Carrascal et al. 1987; Newton 2007; Suárez-Seoane et al. 2008). Although the temporal dimension of biological diversity has not gone unnoticed, changes among temporal periods are rarely addressed (but see Wiens 1989b; Murgui 2007; López de Casenave et al. 2008). These specific responses translate to greater community patterns in accordance with seasonal variation in environmental factors (e.g. Laiolo 2005).

Composition and species richness of avian communities is associated with habitat structure as well as with abiotic factors such as temperature and precipitation; these are directly related to primary productivity, and have been broadly studied, both at local and regional scales and at different periods of the year (Wiens 1989a; Honkanen et al. 2010). However, these studies have mainly focused on landscape and habitat structure parameters during the breeding period, and barely at all on the winter season. Moreover, there is a general lack of fine-grained studies exploring whether the factors ruling the assemblage of local communities remain the same or change throughout the year (but see Carnicer and Díaz-Delgado 2008; Murgui 2010).

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During the breeding season, birds spatially restrict their mating to a central place due to time and energy constraints imposed by incubation and chick rearing duties. Thus, breeding birds show marked habitat preferences in relation to vegetation structure. Specifically, structural complexity of vegetation (tree maturity in forest environments) seems to be the most important attribute determining species richness and diversity at the local scale (Hurlbert 2004; Hinsley et al. 2009). In contrast, during the winter period, when food resources are much scarcer and weather conditions unpredictable, birds adopt a vagabonding lifestyle exploring a greater variety of habitats over larger areas to track the spatio-temporal distribution of food availability (Levey and Stiles 1992; Wiktander et al. 2001). From this perspective, in determining bird distribution at local scales it should be expected that vegetation structure loses importance in winter with respect to the breeding season. Moreover, the ordered gains and losses of species in assemblages, or nestedness (Wright et al. 1998), is hypothesized to decrease in periods of high mobility and relaxed habitat preferences, as is the case during winter time (Murgui 2010).

On the other hand, wintertime air temperatures in temperate zones of the northern hemisphere are below the thermoneutral zone for small birds (usually between 20 and 32 °C; Calder and King 1974; Kendeigh et al. 1977), and the duration of nighttime is considerably longer than that of daytime (approximately 9 vs. 15 h in central Spain during mid-winter). Under these circumstances, wintering birds might respond to spatial variations in temperature, resulting in higher populations observed in warmer areas (Meehan et al. 2004; Carrascal et al. 2012). In addition, species–energy relationships may arise because high-energy areas support more individuals and these larger populations may buffer species from extinction, thus leading to an increase of species richness (the “more-individuals hypothesis”: Hurlbert 2004; Evans et al. 2005). These stressful temperatures do not usually occur in the breeding season, except for sudden frosts and periods of bad weather conditions in early-mid spring that can compromise reproduction success. However, temperatures in the seasonal environments of temperate areas rise from winter minima to high summer temperatures, which can be above the upper critical temperature for small birds (usually above 32–35 °C; Calder and King 1974; Kendeigh et al. 1977). Therefore, we expect birds to avoid the warmest areas in summer in order to reduce overheating and drought stress, a fact that seems to be supported by recent changes in species and assemblages in response to extreme heat waves (e.g. Visser et al. 1998; Sæther et al. 2003; Jiguet et al. 2011).

Under this seasonal environmental scenario in temperate areas, intra-annual variation is foreseeable given both the extent to which bird diversity patterns are explainable by biotic and abiotic factors and the relative importance of thermal environment and habitat structure for the assemblage of local communities. However,

predictions of species richness and distribution, particularly those forecasted under global change by correlative bioclimatic models, typically disregard these seasonal variations. Thus, most prognoses of community change rely on identifying simple, easy-to-measure factors (e.g., average temperature) that are assumed to have constant effects throughout the year (e.g., decreasing diversity; Peterson et al. 2002; Araújo et al. 2006; Pompe et al. 2008).

Here, we explore the seasonality of the avifauna of deciduous forests located in the southwestern Mediterranean region (Central Spain). These montane Mediterranean oakwoods are representative of the most southern broadleaf forests in the southwestern Palearctic Region (Costa et al. 1998), and face dramatic reductions in their extension as a consequence of the predicted climate warming of the coming decades (Sánchez de Dios et al. 2009). Moreover, woodland bird populations in the Iberian Peninsula are peripheral in the geographical domain of the western Palearctic, because a large number of species have their core distribution areas in central and northeastern Europe, with geographical variation of woodland bird species richness decreasing towards southwestern Europe (Tellería and Santos 1993; Mönkkönen 1994; Tellería and Santos 1994; Mönkkönen and Viro 1997; Carrascal and Díaz 2003). According to the abundant-center hypothesis, abiotic determinants of species distribution are more stringent toward the periphery of a distribution range (see a review and a critique in Sagarin et al. 2006). Thus, controls of biodiversity are expected to stand out in these peripheral areas.

Concretely, we study the montane oakwoods of central Spain, with a continental Mediterranean climate characterized by cold winters and warm summers. The mountainous study area offers a considerable environmental heterogeneity, both in orographic characteristics (elevation and cardinal orientations) and in habitat structure (tree maturity, canopy cover, and development of shrub and herbaceous layers; mainly because these forests have been intensively managed for charcoal and cattle grazing). This strong seasonal contrast in abiotic conditions in a heterogeneous woodland environment provides an excellent opportunity to investigate the competing roles of several factors in determining species richness and community assembly at a local scale. The goals of this study are: (1) to relate species richness to orographic, vegetation structure and thermal characteristics of woodlands describing factors (ambient temperature, habitat diversity) and resources (food availability) for forest bird species; (2) to assess how the relationships change between seasons; and (3) to test if the nestedness of bird assemblages is lower in the winter than in the breeding season, considering the relaxed habitat preferences and higher mobility of birds in winter. We hypothesize that species richness and the ordered composition of bird assemblages (i.e. nestedness) will be more associated with variables that are directly related to the energy budget of birds in the more

energetically demanding season (i.e. winter), while the relevance of variables accounting for the onset of breeding, resource use and niche partitioning will stand out during spring. Also, we will briefly discuss the conservation implications of our findings regarding the influence of temperature and vegetation structure on species richness and distribution.

Methods

Study area and period

The study was conducted in the Sierra de Guadarrama region (Madrid province, Central Spain, 40°54'11"–40°33'45"N, 3°46'08"–4°10'03"W), spanning over 500 km² at elevations ranging from 900 to 1600 m a.s.l. Woodland plots were selected in monospecific forests of *Quercus pyrenaica* (a marcescent species typical of southwestern Mediterranean mountains), covering a wide range of variation in forest maturity, elevation and cardinal slope orientations (to account for the amount of incident solar radiation). The climate of the region is continental cold Mediterranean climate, with abundant snowfall and frost in winter (respectively 15 and 49 % of the days in December and January of 2009–2010), and sporadic snowfall and frost in spring (respectively 6 and 9 % of the days in May 2009–2010; data from three neighboring meteorological stations with an average elevation of 1272 m a.s.l.; Spanish Agencia Estatal de Meteorología. Ministerio de Medio Ambiente, y Medio Rural y Marino). We censused a total of 40 plots of 75 m in diameter in winter (December–January) and spring (May) of two consecutive years (2008–2010), focusing on 20 plots each year.

Bird censuses, habitat structure and temperature

We surveyed birds using point count stations (Bibby et al. 2000) lasting 10 min. The settlement period prior to the point count starting was 5 min. All auditory and visual contacts were recorded, but only those within a 75 m (1.77 ha) radius were used in subsequent analyses, because a large proportion (76 %) of the contacts were detected within this census belt. The same trained persons conducted the censuses (LMC and JS) on nearly windless (wind speed < 3 m s⁻¹) and rainless days, within the first 3 h of the morning and in the afternoon beginning 2 h before sunset. We made an effort to improve accuracy in distance estimates, and to reduce inter-observer variability, by training continuously with a laser rangefinder to the cut-off point of 75 m. Plots were separated by at least 300 m to minimize the probability of sampling the same birds more than once, resulting in the nearest oakwood plots being separated by steep ridges. Each year, the censuses were repeated on three different days in December and January (wintering season for all species), and on three different days in May (breeding

season for all species). Thus, each oakwood plot had an accumulated census time of 30 min per season, which is adequate for bird surveys of woodland birds (Shiu and Lee 2003). Species richness was estimated as the average number of forest bird species per 10 min census in the three visits, per plot and season.

Two adjacent 25-m-radius plots were placed within each oakwood plot to sample vegetation structure, representing the environmental heterogeneity within the census plot. Measurements defining vegetation structure were covers of the tree and shrub layers (distinguishing four bush types: oak regrowth < 2 m in height; thorny, fruit producing, shrubs of genus *Crataegus*, *Rubus*, *Prunus* and *Rosa*; *Cistus* spp macchie shrubs; and *Cytisus* and *Genista* brooms), average height of the shrub and tree layers, number of trunks within three diameter classes: 5–10, 10–30 and more than 30 cm at the breast level, average diameter of the 5 thickest oaks, and number of trunks covered by ivy per unit area (see “Appendix” for more details on habitat structure in the 40 study oakwood plots). All vegetation structure variables were visually estimated, after previous training, by LMC and JS and their measurements were averaged for each plot. In addition to structure, leaf development was estimated in May when bird censuses were carried out, as a control of tree phenology (“Appendix”).

To describe local winter and spring air temperatures, one temperature logger (Onset HOBO Pendant, accuracy 0.47 °C) was set in each oakwood plot. Loggers were placed on thick trunks, oriented to the north and at approximately 1.5 m above ground. Data loggers recorded air temperature every 10 min from 01 December to 31 January and from 15 April to 16 June in both study years. For each recording day (144 measurements), midday temperature and minimum night temperature were obtained. Temperatures for the 62 days of the study period were averaged for each oakwood plot (see “Appendix”). Temperature loggers were also set in the 40 woodland plots during 62 summer days from July to August 2010, in order to assess how stressful summer temperatures were in the study area.

Finally, variables summarizing geographical position of the census plots (i.e. elevation and cardinal orientation) were obtained from 1:25000 maps of the Servicio Geográfico Nacional de España. The cosine of the cardinal orientation was used as a description of the northern-southern component of woodland plots ($\cos 0^\circ = 1$, $\cos 180^\circ = -1$), and thus the amount of solar radiation incidence in the study plots.

We controlled for several confounding sampling artifacts and large-scale effects to test contemporary environmental controls on local species richness patterns. First, sampling was done in equal-sized plots within the same habitat type (montane oakwoods), and thus richness estimates were not affected by area inequality (larger areas bias to larger estimates). Additionally, we controlled habitat structure effects on species richness statistically, by including vegetation structure variables in the analyses.

Data analyses

To assess whether the spatial variation in species richness could be attributed to the potential explanatory variables, multiple linear regression models were built with either species richness or nestedness rank of woodland plots as the response variables, using the information-theoretic model comparison approach. Alternative models were compared with Akaike's second-order information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Only those more plausible models with $\Delta\text{AICc} \leq 2$ were selected. Rather than base inferences on a single, selected best model from an a priori set of models, inference was based on the entire set of models using weights (W_i) derived from AICc figures. Such a model-averaged estimator compares favorably in terms of bias and precision with a single estimator that would be extracted from just the best model (Burnham and Anderson 2004). Standardized regression coefficients (β) were obtained in regression analyses as a measure of the sign and magnitude effects of predictor variables (i.e. analyses were carried out with standardized variables, such that their averages are zero and variances are 1). Parameter estimates (β and R^2) were averaged using model weights (W_i) derived from all models with $\Delta\text{AICc} \leq 2$ (Arnold 2010). All the statistical analyses were carried out using STATISTICA 10 (StatSoft Inc, Tulsa, Oklahoma).

Nestedness describes a pattern of orderly impoverishment in species composition by which poor communities are nested subsets of richer communities. These patterns have been attributed to several mechanisms from passive sampling (sites with larger carrying capacities are more likely to accumulate more species) to selective colonization and extinction according to area and isolation of sites, and environmental filtering according to habitat quality and heterogeneity (see a review in Ulrich et al. 2009). In our study, passive sampling was controlled for by the comparison with suitable null models, and nestedness rank could be linked to environmental descriptors compounding habitat quality, whose importance varied between seasons.

Two indexes were calculated to assess assemblage nestedness among the 40 plots on each season: the matrix temperature (T) and the NODF (Nestedness metric based on Overlap and Decreasing Fill), both based on the arrangement of species on a site (rows) by species (columns) matrix (Rodríguez-Gironés and Santamaría 2006; Almeida-Neto et al. 2008). T , which decreases with nestedness, is the most commonly used metric for assessing overall nestedness (Ulrich et al. 2009) and we used it here to facilitate informal comparisons. The newer NODF index has better statistical properties and allows for the quantifying of the separate contribution to nestedness of columns (due to incidence of species) and rows (due to composition of sites; Almeida-Neto et al. 2007). NODF increases with nestedness. The significance of these results was estimated by comparison with null model communities, which were simulated by

randomizing the original presence/absence matrix. Two different null models that incorporate plausible biological structures were tried: c_0 , which randomizes rows and columns in a constrained way to keep column frequencies, and r_1 , which maintains site frequencies and uses column marginal frequencies as probabilities (Jonsson 2001; Moore and Swihart 2007). Thus, null model c_0 accounts for among-species differences (such as different abundances) so that significant nestedness would be attributed to variation in observed richness, while null model r_1 accounts for among-sites differences (such as different carrying capacities) and, partially, for among-species differences, so that significant nestedness would be attributed to variation beyond observed richness or incidence (Moore and Swihart 2007). One hundred randomizations of the matrix were used. We related nestedness rank for sites with environmental variables. These ranks were given as the ordinate in the nestedness plots built with the index T , which are calculated as $(k - 0.5)/n$ for $k = 1 \dots, n$ rows (i.e., the bottom row in the graphs, which is occupied by the more nested site, has a rank of $(1 - 0.5)/40 = 0.0125$). Estimates of nestedness were done with several versions of R (R Development Core Team 2011, versions 2.11 and higher) and the specialized functions of package Vegan (Oksanen et al. 2011, versions 1.17 and higher).

Vegetation predictor variables were synthesized in three vegetation structure factors by means of a Principal Components Analysis with Varimax rotation (PCA, Table 1). The first component (PC1) defines a gradient of oakwood maturity according to its positive relationship with oak height, diameter, density of thick oaks, and presence of ivy and a dense and diverse layer of thorny, fleshy-fruit producing shrubs. The second component (PC2) identifies the woodland plots with a well-developed shrub layer dominated by brooms and oak regrowth. Finally, the third component (PC3) is

Table 1 Principal components analysis performed with 12 variables defining habitat structure in 40 census plots (factors PC1–PC3 obtained after varimax rotation)

	PC1	PC2	PC3
Average shrub layer height	0.28	0.78	−0.10
Cover of thorny, fruit producing, shrubs	0.89	−0.18	−0.02
Cover of oak regrowth (< 2 m in height)	−0.14	0.77	0.02
Cover of brooms (<i>Genista</i> , <i>Cytisus</i>)	−0.10	0.72	−0.13
Cover of <i>Cistus</i> shrubs	−0.17	−0.06	−0.64
Tree layer cover	0.30	−0.19	0.83
Average oak height	0.58	0.24	0.63
Density of oaks 5–10 cm dbh	−0.39	−0.26	0.59
Density of oaks 10–30 cm dbh	−0.42	−0.43	0.66
Density of oaks > 30 cm dbh	0.87	0.17	0.16
Average diameter of the 5 thickest oaks	0.88	0.18	0.09
Number of trunks covered by ivy	0.82	−0.24	0.06
Eigenvalue	3.88	2.23	2.37
% variance accounted for	0.32	0.19	0.20

In bold type, significant correlations between variables and factors (at $P < 0.001$). For more details on vegetation structure variables see “Appendix”

positively related to density and cover of young oaks (< 30 cm dbh).

Results

Species richness

Nearly one half of the observed spatial variation in wintering bird species richness (49.4 %) was explained by an average model including oakwood maturity (first vegetation PCA axis in Table 1) and minimum night temperature as the most influential variables ($\Sigma W_i > 0.8$ and highest magnitude effects; two models with $\Delta AICc \leq 2$; Table 2). Winter species richness increased in parallel to minimum night temperature and oakwood maturity (Fig. 1).

Spatial variation in species richness during the breeding season was explained to a greater degree (model average of 64.5 % of variance) by the eight

predictor variables (seven models with $\Delta AICc \leq 2$; Table 2). The variables most affecting spring species richness ($\Sigma W_i > 0.8$) were elevation (with the highest magnitude effect β), density and cover of young oaks (PC3 in Table 1), development of oak leaves and average temperature at midday: species richness decreased with increasing elevation, midday temperature and density of young oaks, and increased with advanced development of young oak leaves the second fortnight of May (Fig. 2). Cardinal orientation of oakwoods (lower species richness at northern slopes), oakwood maturity (positive effect, first vegetation PCA axis in Table 1) and development of dense shrub layer of oak undergrowth (negative influence) had a marginal role in determining bird species richness during the breeding season.

There were marked changes in the influence of predictor variables between seasons, as shown by evidence ratios (quotient of variables' weights in models of Table 2; we focus here on evidence ratios > 7 in variables with weights > 0.33 at either season). Average

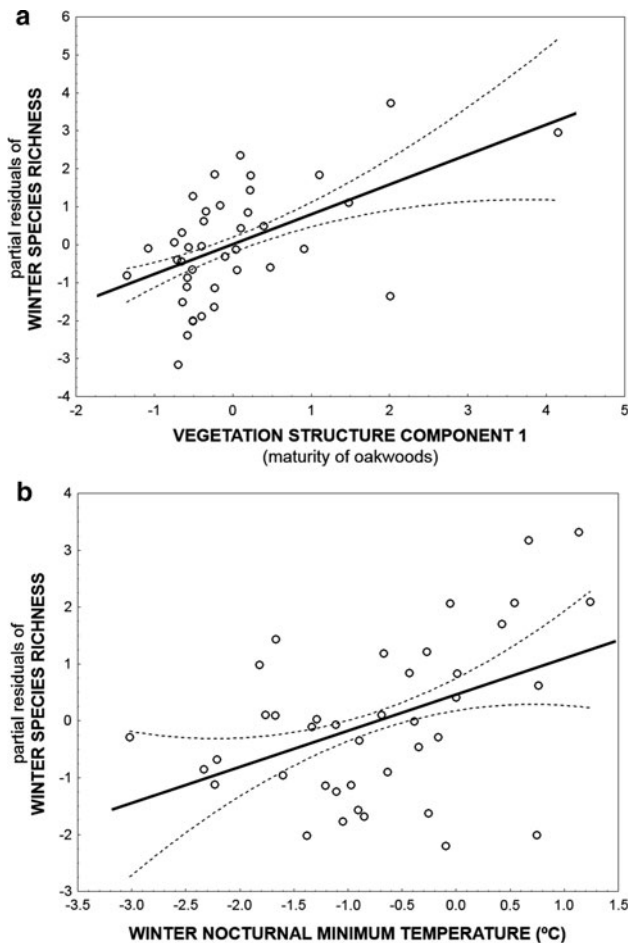


Fig. 1 Partial residual plots illustrating the influence of oakwood maturity (a) and winter nocturnal minimum temperature (b) on winter species richness in 40 oakwood plots of central Spain in two consecutive winters (2008–2010). Residuals are calculated by keeping the other predictor variables except oakwood maturity and minimum temperature, respectively, at their means, thus partialling out their effects

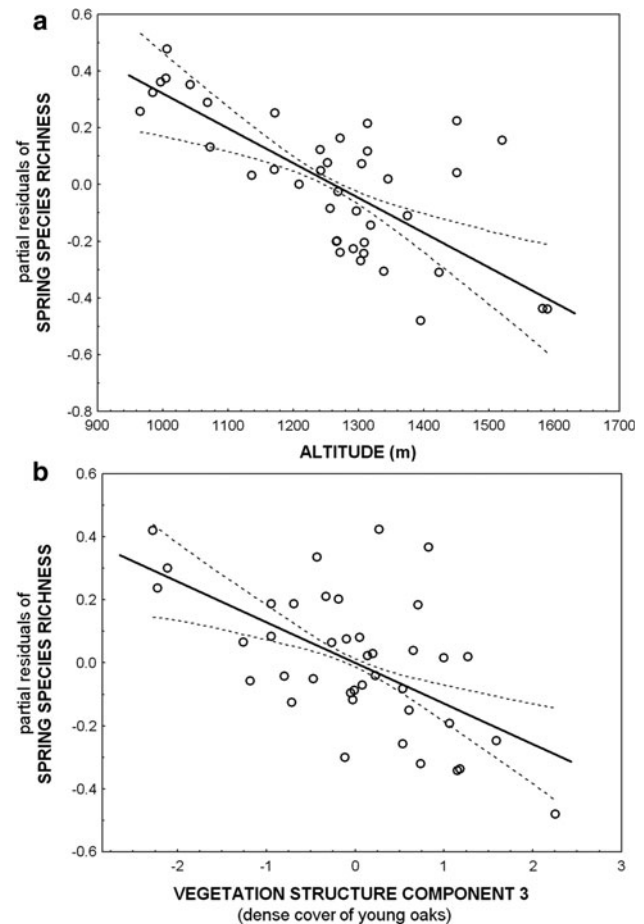


Fig. 2 Partial residual plots illustrating the influence of elevation (a) and the dense cover of young oaks (b) on spring species richness in 40 oakwood plots of Central Spain in two consecutive years (2009–2010). Residuals are calculated by keeping the other predictor variables except elevation and cover of young oaks, respectively, at their means, thus partialling out their effects

minimum nighttime temperature (positively) was only influential during winter, while elevation and northern cardinal orientation (both negatively) were only influential during spring. In addition, cover of young oaks (negatively) was very influential during the breeding season and had a null effect in winter. Although less clearly related to richness, midday temperature had opposite effects in winter (positive) than in spring (negative).

Nestedness

Both winter and spring assemblages were moderately but significantly nested. Winter assemblages (with a matrix fill of 0.26) had $T = 17.8$ ($P_{r1} = 0.049$, $P_{c0} = 0.001$) and $NODF = 58.1$ ($P_{r1} = 0.001$, $P_{c0} = 0.001$). The contribution of woodland plots (rows) to $NODF$ was larger than the contribution of species (columns; 66 vs. 51). Spring assemblages (with a matrix fill of 0.33) had a higher $T = 31.4$ ($P_{r1} = 0.001$, $P_{c0} = 0.123$) and almost the same $NODF = 58.9$ ($P_{r1} = 0.001$, $P_{c0} = 0.041$), which suggests a less ordered matrix (i.e. less nested). Again, the contribution of woodland plots (rows) to $NODF$ was larger than that of species (columns; 61 vs. 51). Matrix size and fill were moderate, which means that T estimates are less prone to type-I error (Ulrich and Gotelli 2007).

Nestedness patterns are related to the analyzed explanatory variables (see Akaike multimodel inference

in Table 3). In winter assemblages, the predictors explained an average of 43 % of the variation in nestedness rank (six models with $\Delta AICc \leq 2$). Larger contributions were made by temperature (both midday and minimum nighttime temperatures) and the first vegetation PCA axis (oakwood maturity), all with a negative effect on the nestedness rank. Therefore, colder and younger woodland plots in winter showed an orderly impoverishment in species composition. In spring assemblages, a similar average proportion of the variation in nestedness rank was explained by the descriptors (40 %; four models with $\Delta AICc \leq 2$; Table 3). In this case, larger contributions were made by elevation (with a positive effect on nestedness rank), oakwood maturity (PC1, with negative effect), the development of a dense shrub layer of brooms and oak regrowth (PC2), and the cover of a dense layer of young oaks (PC3; the last two factors with a positive effect on nestedness rank). Thus, communities in spring displayed a gradual impoverishment in young forests with a dense shrub layer located at high elevations.

The most remarkable seasonal differences in the influence of environmental predictors on the orderly impoverishment in species composition of bird assemblages were: (1) the high importance of elevation in spring and its null influence during winter, (2) the higher influence of temperature in winter compared to spring, (3) and the higher importance of all vegetation structure components in spring compared to winter (compare Akaike weights in Table 3 between both seasons).

Table 2 Alternative models for species richness of birds in 40 oakwood plots of central Spain in winter and spring of two consecutive years (2008–2010), ordered by the value of the AICc criterion (with small sample correction)

Winter	PC1	TNOCT	TZENIT	ELEVATION	ORIENT	PC2	PC3	LEAF INDEX	R^2 (%)	W_i	AICc
Standardized regression coefficients (β)											
Model 1	0.45	0.36							49.2	0.70	136.3
Model 2	0.44	0.32	0.08						49.7	0.30	138.0
Weighted average											
β	0.45	0.35	0.02	0.00	0.00	0.00	0.00	–	49.4		
ΣW_i	1.00	1.00	0.30	0.00	0.00	0.00	0.00	–			
Spring	ELEVATION	PC3	LEAF INDEX	TZENIT	ORIENT	PC1	PC2	TNOCT	R^2 (%)	W_i	AICc
Standardized regression coefficients (β)											
Model 1	–0.72	–0.41	0.30	–0.27	–0.19				64.1	0.22	149.8
Model 2	–0.72	–0.40	0.34	–0.25	–0.20		–0.18		67.2	0.17	150.3
Model 3	–0.61	–0.41	0.34	–0.24					61.6	0.16	150.4
Model 4	–0.47	–0.40	0.30	–0.21		0.25			65.7	0.15	150.6
Model 5	–0.61	–0.41	0.38	–0.23			–0.18		64.4	0.12	151.0
Model 6	–0.39	–0.32	0.28			0.28			62.6	0.10	151.3
Model 7	–0.56	–0.40	0.29	–0.23	–0.12	0.21			66.6	0.09	151.6
Weighted average											
β	–0.60	–0.40	0.32	–0.22	–0.08	0.08	–0.05	0.00	64.5		
ΣW_i	1.00	1.00	1.00	0.90	0.47	0.33	0.29	0.00			

Only those models with an increase in the AICc statistic ≤ 2 are shown. Figures for each variable are beta regression coefficients obtained in general linear models

ΣW_i sum of weights of the models in which the variable appears, R^2 variance explained by each model (in %); W_i model weight. *PC1*, *PC2* and *PC3* habitat structure components (see Table 1), *TNOCT* average minimum nocturnal temperature, *TZENIT* average midday temperature, *ORIENT* cosine of the cardinal orientation of each woodland plot defining a north (positive) to south (negative) vector, *LEAF INDEX* average oak leaf development on 2nd fortnight of May (not possible to analyze in winter time due to the lack of foliage in that season)

Table 3 Alternative models for nestedness rank of bird composition in 40 oakwood plots of central Spain in winter and spring of two consecutive years (2008–2010), ordered by the value of the AICc criterion (AIC with small sample correction)

Winter	PC1	TZENIT	TNOCT	ORIENT	ELEVATION	PC2	PC3	LEAF INDEX	R ² (%)	W _i	AICc
Standardized regression coefficients (β)											
Model 1	-0.25	-0.25	-0.35						46.2	0.26	1.15
Model 2	-0.27		-0.46						41.8	0.21	1.58
Model 3	-0.39	-0.38							38.6	0.16	2.16
Model 4	-0.36	-0.44		-0.19					41.8	0.15	2.28
Model 5		-0.27	-0.47						41.5	0.13	2.52
Model 6	-0.26	-0.29	-0.31	-0.10					47.0	0.10	2.96
Weighted average											
β	-0.26	-0.25	-0.28	-0.04	0.00	0.00	0.00	-	42.9		
ΣW_i	0.87	0.79	0.70	0.25	0.00	0.00	0.00	-			
Spring	ELEVATION	PC1	PC2	PC3	TZENIT	LEAF INDEX	TNOCT	ORIENT	R ² (%)	W _i	AICc
Standardized regression coefficients (β)											
Model 1	0.39	-0.24	0.16	0.25					41.5	0.41	3.19
Model 2	0.42	-0.22	0.17						35.1	0.25	4.15
Model 3	0.45	-0.22	0.15	0.31	0.15				43.0	0.18	4.79
Model 4	0.36	-0.20	0.22	0.27		-0.22			45.6	0.15	5.16
Weighted average											
β	0.41	-0.23	0.17	0.20	0.03	-0.03	0.00	0.00	40.8		
ΣW_i	1.00	1.00	1.00	0.75	0.18	0.15	0.00	0.00			

Only those models with an increase in the AICc statistic ≤ 2 are shown. Figures for each variable are beta regression coefficients obtained in general linear models

ΣW_i , the sum of weights of the models in which the variable appears, R² variance explained by each model (in %), W_i model weight. PC1, PC2 and PC3 habitat structure components (see Table 1), TNOCT average minimum nocturnal temperature, TZENIT average midday temperature, ORIENT cosine of the cardinal orientation of each woodland plot defining a north (positive) to south (negative) vector, LEAF INDEX average oak leaf development on 2nd fortnight of May (not possible to analyze in winter time due to the lack of foliage in that season)

Discussion

Spatial variation in bird species richness of these montane Mediterranean forests is a deterministic phenomenon both in winter and spring. Our results support the notion that patterns of biodiversity can be explained successfully at a fine-grained scale not only by habitat structure variables, but also by abiotic factors summarizing the thermal environment, which are more frequently linked to larger scales (Honkanen et al. 2010; Jiménez-Valverde et al. 2011). We hypothesized that habitat structure would be the prominent factor defining habitat preferences during the breeding season (Wiens 1989a), while temperature would be prominent in winter because it affects individual energetics through the increased physiological costs of low winter temperatures, and such constraint predominates over other biotic processes that might also influence distributions (Meehan et al. 2004; Evans et al. 2006). We indeed found that determinants of fine-grained patterns of bird species richness and nestedness of bird assemblages in the studied oakwoods were very different between seasons. This disparity highlights the importance of understanding the mechanisms underlying specific spatial and temporal scenarios when interpreting biodiversity patterns. Moreover, the explained differences in the variation of species richness turned out to be lower in winter (49.4 %) than in spring (64.5 %). The harsh winter environmental conditions, together with the vagabonding lifestyle of

birds during this period directed at confronting low resource availability, cold spells and sudden periods of bad weather conditions (Fretwell 1972), should cause species richness to be less deterministic in winter.

Spring and winter assemblages are moderately but significantly nested, with higher nestedness of bird communities in winter than in spring. Murgui (2010) and Fernández-Juricic (2000) studied Spanish urban parks and also found a nested pattern in bird communities during the breeding season. However, in contrast to our results on natural montane forests, which show more marked seasonal changes and where winter is harsher, Murgui (2010) found no nestedness in wintering communities of coastal parks. In that study, some species moved from parks to forage and found refuge in the surrounding urban matrix, a strategy that contributed to the nested pattern but that was not available for birds living in natural forests.

Nestedness was weaker for species than for sites, so it is more likely due to site properties (environmental conditions, habitat quality, habitat nestedness) than to species characteristics (local abundances or mass effect; Calmé and Desrochers 1999; Hylander et al. 2005; Almeida-Neto et al. 2008). These results are in agreement with the nested habitat quality hypothesis, which states that gradients of environmental harshness are a cause of nested subset patterns in communities because of differences in tolerance to the deficiency of a resource or condition among the species (Hylander et al. 2005). On the other hand, nestedness may additionally be promoted

by some specialized species or guilds whose abundances are tightly related to habitat structure gradients, such as trunk foragers that are more dense in mature oakwoods and rare or absent in younger stands (see Carrascal and Díaz 2006; Roberge and Angelstam 2006; Caprio et al. 2009; for deciduous managed forests in Europe). Therefore, our results show that seasonality influences patterns of ordered gains and losses of species in bird assemblages where environmental characteristics are of higher importance than those related to particular species.

Air temperature has an opposite effect in structuring oakwood bird diversity in winter and in spring. Minimum night temperature has an important positive effect in winter species richness and in the orderly enrichment of winter communities, while having a null effect in spring (Tables 2 and 3). This might reflect the energetic constraints suffered by birds during long winter nights (14 h 41' on 01 January in the study area), when environmental temperatures fall well outside the thermoneutral range for small passerines (usually between 20 and 32 °C; Calder and King 1974; Kendeigh et al. 1977). Under these high thermoregulation costs, a variation of 4.2 °C in night temperature among woodland plots (ranging from -3.0 to 1.2 °C, "Appendix") can make the difference and thus determine winter species richness through residency-area selection. This is not relevant in spring, when the duration of night is shorter (9 h 32' on 15 May in the study area), night temperatures are considerably higher (see "Appendix"), and thermoregulation costs are consequently reduced.

Contrary to night temperature, midday temperature has an important negative effect on spring species richness and an almost null effect on winter (Table 2). The negative effect of midday temperatures in spring may reflect future temperature stress at summertime. Midday spring temperature during the study period was not determined to be stressful (variation of 16.4–23.1 °C among the 40 woodland plots), while in summer, mean midday temperature was 27.7 °C (range 24.3–31.0 °C in July and August) and temperature went over 30 °C for an average of 123 h per plot (range of 0.5–346.2 h; data obtained during 62 days on July to August-2010). Moreover, summer and spring midday temperatures were highly correlated across the 40 study woodland plots ($r = 0.686$). Thus, the negative effect of midday spring temperatures could be related to summer residence and the prevention of high temperatures and water stress in the warmest season (Williams and Tieleman 2000; Tieleman and Williams 2002), an in-advance response to summer stress in these forests. There is a great deal of evidence of the influence of the recent increase in ambient temperatures on the breeding biology of many bird species, both at local and large spatial scales (Visser et al. 1998; Sanz 2002; Sæther et al. 2003; Visser 2008). Increasing temperatures have led to important changes in the onset of breeding, clutch size and hatching and fledging success in Mediterranean montane populations of several passerine species inhabiting oakwoods in central Spain, with mismatches between the timing of peak

food supply, nestling demands and fewer young fledging with warmer temperatures (Sanz et al. 2003; Potti 2008, 2009). Therefore, we postulate an impoverishment of breeding bird communities in these forests if spring and summer temperatures continue to increase in the future (I.P.C.C. 2007; Brunet et al. 2009), especially at lower elevations where higher temperatures and higher current species richness are found.

Elevation is the most important factor governing species richness and nestedness in spring, while having a complete null effect in winter: elevation has a marked negative effect on both species richness and the nested enrichment of communities in spring (see in Tables 2, 3 the sum of Akaike weights and standardized partial regression coefficients, after controlling for temperature, vegetation structure and orographic factors). Due to its inverse relationship with temperature (the adiabatic lapse rate), and the negative effect of temperature on species richness during the breeding season, we could expect an increase in species richness at higher elevations. Moreover, recent climate warming has been shown to induce upward elevational shifts of the distributional range of several species that track favorable abiotic conditions (Parmesan and Yohe 2003; Sekercioglu et al. 2008; Maggini et al. 2011; but see Archaux 2004; Popy et al. 2010). The positive relationship between elevation and species richness at a local scale is also predicted considering the general biogeographic pattern observed for birds in the Iberian Peninsula at larger spatial scales: the frequency of occurrence of species belonging to the European, Palaearctic and Holarctic biogeographic groups are usually positively associated with elevation (Carrascal and Díaz 2003). This result may respond to a conservative strategy during the breeding season, when parental investment is most at risk. At higher elevations climate instability increases, with a corresponding rise in cold spells and snowfalls (0 vs. 9 days of frosts and 0 vs. 2.25 days of snowfalls per month in May 2009 and 2010, in lower versus higher meteorological stations; Spanish Agencia Estatal de Meteorología; Ministerio de Medio Ambiente, Medio Rural y Marino; data for four meteorological stations located at 925–1160 and 1532–1894 m a.s.l.). These unpredictable events may compromise incubation and breeding of woodland birds in the mountainous areas by both suddenly decreasing air temperatures and reducing food availability (see Sanz and Moreno 1995 for a food provisioning experiment in a population of *Ficedula hypoleuca* breeding at high elevation in central Spain). Therefore, it seems that the commonly proposed strategy of altitudinal migration to escape from global warming effects is not that simple, as birds depend on climatic variables other than temperature (La Sorte and Jetz 2010).

Relationships between vegetation variables (of habitat structure and phenology) and bird community parameters (species richness or nestedness) seems to be stronger in spring than in winter. Moreover, the relative relevance of each habitat structure component depends on the season. In winter, forest maturity is the only

relevant component of vegetation structure for bird species richness, and maturity governs the ordered appearance of species throughout these monospecific forests. Forest maturity is also related to nestedness in the breeding season, in concordance with Fernández-Juricic (2000). Nevertheless, young tree cover negatively affects species richness during this season, being the most important factor with regard to vegetation structure. This result highlights the importance of oak regrowth clearance and thinning (the reduction of the high density of young oaks) in young forests, in order to avoid forest monotony and to increase the heterogeneity of the understory layer. These silvicultural practices will allow a higher penetrability of potential breeding birds of Mediterranean forests contributing to the diversification of the avifauna (De la Montaña et al. 2006).

The phenology of leaf development has an important influence on bird species richness in the studied oakwoods. Leaf development is tightly related to the reproductive phenology of birds through the availability of arthropods (mainly caterpillars) that depend on temporal changes in the amount and quality of foliage (Van Balen 1973; Forkner et al. 2004). The coupling of the maximal peak in food abundance to the peak in chick feeding demands has important consequences for reproductive success of woodland birds (Van Noordwijk et al. 1995; Buse et al. 1999). Our result completely agrees with a number of studies on these species in the Palaearctic Region that have found a tight correlation between an early breeding date and reproductive success (for instance, see Sanz 1999 for Blue tit, *Cyanistes caeruleus* and Barba et al. 1995 for Great tit, *Parus major*). These two points imbricate the mechanism by

which oakwoods with an earlier tree leaf development are preferred by birds, showing higher species richness.

In conclusion, determinism and determinants of bird species richness and community species losses along environmental gradients in montane Mediterranean oakwoods depends highly on the season, highlighting the importance of understanding the mechanisms underlying specific scenarios when interpreting biodiversity patterns. Winter is the season when species richness and community nestedness are less deterministic, the only important factors being forest maturity and minimum night temperature: wintering birds prefer mature forests with higher nocturnal temperatures where they can minimize thermoregulation costs during the most stringent hours. Bird species richness and community nestedness are more deterministic in spring when birds prefer cooler forests at midday, located at lower elevations, with a lower density of a monotonous undergrowth layer of young oaks and an advanced tree leaf development where reproduction can be initiated earlier. Even in the more energy-favorable period, parental investment seems to be threatened by sudden cold spells associated with higher elevations or high midday temperatures both during the breeding season and the summer.

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Appendix

See Table 4.

Table 4 Mean and range (min/max) of study variables in 40 oakwood plots in central Spain during winter and spring of two consecutive years (2008–2010)

	Mean	Min/max
Cumulative number of bird species (in 3 censuses); winter	6.6	1/15
Cumulative number of bird species (in 3 censuses); spring	12.9	8/19
Average number of bird species (in 3 censuses); winter	3.1	0.3/8
Average number of bird species (in 3 censuses); spring	8.2	4/13.3
Elevation (m)	1260	965/1597
Cardinal orientation (° to north)	144	1/358
Average air temperature at midday (°C); winter	5.5	3.4/7.1
Average air temperature at midday (°C); spring	19.9	16.4/23.1
Average minimum night temperature (°C); winter	−0.75	−3.0/1.2
Average minimum night temperature (°C); spring	9.2	6.1/11.9
Cover of thorny, fruit producing, shrubs (<i>Crataegus</i> , <i>Rubus</i> , <i>Rosa</i> , ...) (%)	4.4	0/45
Cover of maquis (<i>Cistus</i>) shrubs (%)	3.7	0/52
Cover of brooms (<i>Cytisus</i> and <i>Genista</i> shrubs) (%)	6.4	0/37
Cover of oak regrowth (< 2 m in height) (%)	5.3	0/50
Average shrub layer height (m)	1.0	0.0/2.40
Tree layer cover (%)	64.2	24/90
Average oak height (m)	11.7	6/17
Density of small sized oaks (trunks 5–10 cm dbh per ha)	508	31/2098
Density of medium sized oaks (trunks 10–30 cm dbh per ha)	687	145/2292
Density of large sized oaks (trunks > 30 cm dbh per ha)	29	0/158
Average diameter of the five thickest oaks (cm)	32	19/55
Number of trunks covered by ivy (per ha)	22	0/357
Oak leaf index (average on 2nd fortnight of May)	4.6	2.3/5.7

Number of bird species refer to census plots 75 m in diameter

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