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Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean

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ABSTRACT

Teasing out how species respond to human-induced environmental changes has become a priority for addressing the challenges posed by the need to conserve biodiversity. Although land abandonment is widespread, the threat it can represent to biodiversity remains poorly understood. To address this issue, we used data from eight long-term studies in a region with widespread land abandonment that has been identified as a biodiversity hotspot, the north-west Mediterranean Basin. We conducted a multi-site analysis of how changes in species occurrence were affected by species' attributes (habitat preference, habitat breadth, migration strategy and latitudinal distribution). The analysis revealed a nested pattern in the effect of species attributes. Woodland and shrubland species showed the strongest increase, whereas no change in overall occurrence patterns was detected in farmland species. Residents increased significantly, especially those with a northern distribution, whereas migrants decreased significantly, especially farmland species with a narrow habitat breadth. Changes in species occurrence were also related to initial landscape composition, with larger increases in initially woodland or mixed landscapes. Woodland species increased in all landscape types, shrubland species increased only in mixed landscapes, and farmland species decreased more, although not significantly, in farmland landscapes. Our results strongly support the hypothesis that large-scale habitat changes associated mainly with land abandonment are impacting bird community patterns in the Mediterranean region. Negative effects seem to be recorded mostly for migrants in farmland landscapes, suggesting that declines in these species are likely to be caused by a variety of mechanisms interacting with habitat change in the breeding region.

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1. Introduction

In the context of large-scale, human-caused changes, ecology aims at understanding the responses of ecosystems and species to temporal changes in habitat structure and composition. This understanding may then be used to improve both our knowledge of fundamental biological processes and our successful implementation of conservation policies. Land abandonment, although less publicised than land use intensification, is a major consequence of the current socio-economic context prevailing in highly industrialized countries. Abandonment is widespread in several regions of North America (Parody et al., 2001), as well as in mountain regions of eastern and southern Europe (Ostermann, 1998). Decreasing human impact primarily affects the least productive agricultural lands and triggers a recovery of semi-natural vegetation. In Europe, however, whole suites of species with high conservation profiles are associated with traditional land uses and with the human-maintained semi-natural habitats they produced. Many of these species are considered to be threatened by current changes in land use (Ostermann, 1998), including agricultural abandonment.

The Northern Mediterranean Basin has a particularly long and complex human history, which has helped to shape its habitats and fauna. It is considered to be a biodiversity hotspot (Myers et al., 2000), but has recently experienced fast and widespread agricultural abandonment (Mazzoleni et al., 2004) which is thought to be a major cause of species declines, especially in bird communities (Farina, 1995, 1997). Despite rather intensive biological monitoring in this region (Blondel and Aronson, 1999), only a limited number of studies have investigated the biological consequences of agricultural abandonment, especially at a regional scale (Mazzoleni et al., 2004). Among the small number of existing quantitative studies, those considering changes in bird species occurrence at different scales provide a valuable opportunity to investigate the processes involved in species' responses to land abandonment and to test different hypotheses about the mechanisms involved.

The recovery of semi-natural vegetation that results from agricultural abandonment causes a decrease of farmed or grazed open habitats and an increase in shrubland and woodland cover (Debussche et al., 1999; Romero-Calcerrada and Perry, 2004). This should favour an increase in the occurrence of woodland bird species and a decrease in the occurrence of those tied to open farmland habitats (see e.g. Preiss et al., 1997; Suarez-Seoane et al., 2002; Sirami et al., 2007).

Since habitat specialists are likely to depend on specific landscape elements (Tews et al., 2004), they are expected to be more sensitive to changes in landscape structure (Bender et al., 1998). Farmland specialists should therefore be more affected than farmland generalists by a decrease in the amount of farmland habitat in the landscape. Woodland generalists should benefit more from land abandonment than woodland specialists, at least initially.

Other studies have suggested that migrant bird species might be more sensitive to habitat changes than resident species (Sol et al., 2005). Böhning-Gaese and Bauer (1996), for example, documented that migrants had significantly more negative population trends than residents in a central European region. Sanderson et al. (2006) hypothesized that such negative population trends resulted more from changes that occurred along the migration routes or on the wintering grounds in Africa than from changes in the breeding grounds. Migrants from the Mediterranean region are likely to be subjected to the same non-local factors. Negative effects on populations caused by changes on the breeding grounds may therefore combine with negative effects related to factors operating during migration and/or on the wintering grounds. If the impact associated with long-distance migration is more negative than the impact associated with wintering in Europe as suggested by Sanderson et al. (2006), we should expect migrants to have, on average, less favourable population trends than residents in all habitats, and migrants tied to open habitats to be more affected than migrants tied to woodlands.

Finally, in the Mediterranean region, bird communities are characterized by a combination of Mediterranean endemics, mostly associated with the more open habitats, and of Eurasian species associated mostly with forested habitats (Blondel and Farre, 1988). In the case of land abandonment driving bird species trends, landscape changes originated by land abandonment should have a stronger positive effect on the occurrence of species with a more northerly distribution than of species with a more southerly distribution. An alternative hypothesis could be the impact of climate change on bird populations. Where climate change effects dominate, we should expect southern species to increase in line with their preference for areas with higher temperatures. This should be favored by the general trend towards climate warming experienced in the western Mediterranean particularly during the last two decades (Moisselin et al., 2002).

Bird species' responses to land abandonment should also be affected by the initial nature of the overall landscape subjected to land abandonment, and vary according to whether the initial landscape is dominated by farmland, shrubland or woodland, or is a mixed landscape. This could be particularly true for shrubland species, which should, at least temporarily, be favoured by agricultural abandonment in a landscape that initially had a significant area of farmland and grazed areas, but be negatively affected in a landscape initially dominated by shrubland that will more rapidly change into denser woodland (see e.g. Sirami et al., 2007).

To test these hypotheses on the effects of land abandonment on bird species in the Mediterranean region, we used data from eight long-term studies that investigated changes in habitats and songbird populations at the landscape scale. Using meta-analytical techniques, we conducted a multi-site analysis of the temporal data collected in the eight landscape-scale studies available in the north-western Mediterranean Basin. The goal was to test two sets of predictions on species' responses. The first set dealt with the effects of species' biological attributes: habitat preference, habitat breadth, migration strategy and mean latitudinal distribution. The second set referred to the effect of the initial landscape characteristics on bird species' responses.

2. Methods

2.1. *Studies and bird species selection*

We searched for published and unpublished datasets that provided quantitative information on changes in bird communities in a Mediterranean landscape that has been affected by land abandonment. We restricted our search to the four main countries in the north-western Mediterranean Basin (Portugal, Spain, south of France and Italy) that share relatively similar socio-economical contexts. Study sites were required to meet the following criteria. First, they had to experience a local context of land abandonment (rural depopulation, decrease of wood exploitation and grazing), leading to a decrease of farmland habitats and an increase in forest cover (Mazzoleni et al., 2004). Second, they had to be located in areas with a truly Mediterranean climate (Blondel and Aronson, 1999); hence, we excluded data from high mountain areas (i.e. above 2000 m). Third, the sites had to managed traditionally as agro-forest systems, i.e. consisting of landscapes composed of non-intensive crops and grasslands, grazed or ungrazed shrublands and woodlands. Extensive areas covered by urban fabric or irrigated crops were excluded. Fourth, each dataset had to document bird species occurrence in a series of sampling plots describing species presence/absence for two dates over a time period matching strong socioeconomic changes that led to widespread abandonment of traditional agricultural activities in the study region under interest (e.g. Preiss et al., 1997). Bird species occurrence had to be assessed either by point-count censuses or by line transects. We excluded any study that documented only an overall occupancy rate or an overall abundance index. Finally, each dataset was included only if it provided enough detailed information on initial landscape composition.

We found eight such studies matching the selected criteria. They were located in only two of the focal countries, France and Spain (Table 1 and Fig. 1). Study sites from Spain were obtained from geographical subsets of the Catalan Breeding Bird Atlas (Estrada et al., 2004) according to the predefined criteria above.

We excluded birds of prey, as the point-count censuses used in most of the studies are not designed to assess their abundance. We also excluded waterbirds, seabirds and birds tied to rocky or urban areas, as their distribution is likely to be affected by factors other than vegetation changes (e.g. human activities). We also excluded species observed within a site if fewer than five occurrences were recorded during both time periods. We also excluded species observed in only one study site.

2.2. *Estimation of effect sizes*

Meta-analysis is a powerful quantitative method to combine and analyse several datasets that address the same hypotheses in order to determine whether they share a common statistical relationship and whether this relationship is related to one or several predictor variables. In our case, we wanted to determine whether bird species shared a common temporal trend in the different study sites, and whether this trend was related to the predictor variables. Because the results from different studies are measured on different scales, which can give rise to heterogeneity in the results (Osenberg et al., 1999), the dependent variable in a meta-analysis is some standardized measure of effect size. In our case, effect size was defined as the degree of change in bird species occurrence between two periods (correlation coefficient r). For each species on each study site, we obtained the chi-square coefficient of generalized estimating equations (GEEs: extensions of generalised linear models for binary repeated data; Lipsitz et al., 1994) to estimate correlation coefficients (with S-Calculator in MetaWin version 2.0; Rosenberg et al., 1997) that reflected the strength of the changes in species occurrences. Correlation coefficients and procedures for calculating and combining effect sizes based on r are widely used in meta-analyses (e.g. Brotons et al., 2003; Lampila et al., 2005). The sign of the correlation ratio indicates the direction of the change. A positive effect size indicated that the occurrence of a species was higher during the second study period and vice versa. We normalized effect sizes obtained for individual species with the Fisher's transformation of r, Zr.

Table 1 – List of study sites considered in the multi-site analysis

Site	T1	T2	Time period	Area (ha)	Sample size	Landscape	Refs.
1. Tarragona	1975–1983	1999–2002	21	830,000	83	Farmland	Estrada et al. (2004)
2. Girona	1975–1983	1999–2002	21	780,000	78	Woodland	Estrada et al. (2004)
3. Leida	1975–1983	1999–2002	21	860,000	86	Mixed	Estrada et al., 2004
4. Causse	1982–1987	2001–2002	17	10,000	214	Farmland	Lovaty (1997) and Fonderflick (unpublished data)
5. Corsica	1987	2003	16	891	142	Mixed	Coreau and Martin (2007)
6. Lubéron	1976–1978	2003–2004	26	14450	198	Farmland	Olioso and Hameau (unpublished data)
7. Mont Ventoux	1973–1974	2000–2001	27	20000	160	Woodland	Archaux (2002)
8. Pic Saint Loup	1978	2003	25	2800	194	Woodland	Sirami et al. (2007)

T1 and T2, years of the first and second census; time period, number of years between the median of the two censuses; area, area covered by the study site (measured in hectares); sample size, number of stations censused in the study site; landscape, type of landscape; and Ref., reference source.

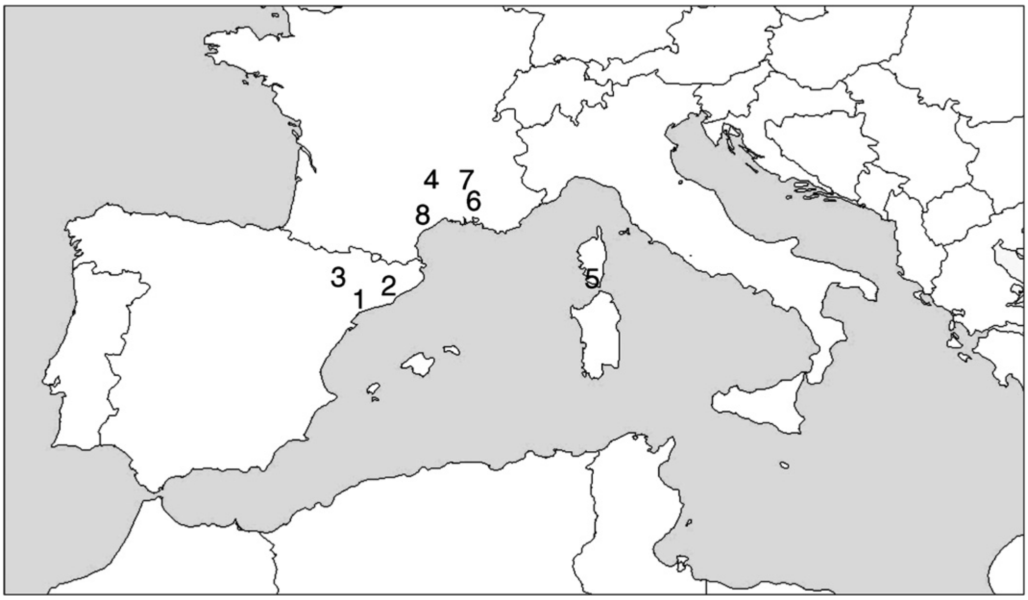

Fig. 1 – Map of the eight study sites (numbers correspond to study sites numbered in Table 1).

2.3. Models

To analyse the long-term effects of land use changes, we combined estimates of effect size obtained for individual species by using the procedures used by Lampila et al. (2005). We considered that the effect size estimate for each species was drawn from an underlying distribution of effect sizes, rather than being an estimate of a single, common effect size. Thus, for all hypothesis tests, we used fitted random-effects models, equivalent to a mixed effects linear model, with fixed effects as covariates; the random effect was the deviation of the true effect size of a species within a study from the value predicted by the model (Gurevitch and Hedges, 1999). In order to control for a potential effect of sample size and give more weight to estimates obtained from larges samples, we used weighted averages of effect sizes within various categories; these were obtained by weighting effect sizes by their variances. For random-effects models, this consisted of weighting Zr values by the reciprocal of the sum of their conditional variance and the between-study variance (for details, see Brotons et al., 2003; Lampila et al., 2005). All meta-analytical procedures were performed with MetaWin software.

2.4. Analysis

We checked that the characteristics of the sampling methods from the different studies (length of the period and area covered, number of stations sampled) had no effect on the changes in bird species occurrence measured in the different studies. We classified the eight studies into three groups according to: the time period covered (<20 years, 20–25 years, >25 years); the surface examined (<10,000 ha, 10,000–100,000 ha, >100,000 ha); and the sample size collected in each study (<90, 90–180, >180 sampling units).

First, we tested whether the species' biological attributes had an effect on the strength of their responses to land abandonment. We obtained information on habitat preferences from Tucker and Evans (1997) and grouped species into three categories: "farmland" refers to both cultivated and grazed open habitats; "shrubland" refers to open to closed shrublands; and "woodland" refers to open woodlands to closed forests (variable habitat preference). When a species was associated with two or three preferred habitats, we considered the species to be associated with each preferred habitat, but the effect size corresponding to this species was weighted respectively by 1/2 or 1/3.

To obtain a measure of habitat breadth, we developed an index from species habitat selection patterns at the landscape scale, as described in the Catalan Breeding Bird Atlas (Estrada et al., 2004). In this work, an extensive presence/absence bird species sampling of 1 × 1 km squares was conducted from 1999 to 2002 (i.e. 3077 squares), including a description of landscape composition for each square. Based on species habitat selection patterns, we first performed a matrix of Pearson distances between all measured habitats. To describe how distant these habitats were from each other in terms of species' relative use, this matrix was then employed to estimate an overall ecological distance between the different Atlas habitat categories. Finally, the habitat breadth index was obtained by summing up these distances (weighted according to the relative use of each habitat by species) for all habitat categories in which each species was present. Our habitat breadth estimation procedure has the interesting propriety of not assuming that differences between two given habitats are the same, irrespective of the nature of these habitats, but that they are a function of how bird communities differ between them. Furthermore, it is worth noting that this habitat breadth index is based on 1 × 1 km resolution data and should be interpreted as an index of the range of broad habitat categories in which a given species is present, rather than as a measure of the range of vegetation structure used. In particular, species with a narrow selection of vegetation structure (i.e. narrow niche breadth) but which can use such structures in a wide variety of contexts within different bird communities (e.g. in different types of shrubland, or in shrublands, alpine grasslands and farmlands) have a broader index than species with a narrow vegetation structure selection (e.g. only in natural, low altitude shrublands or woodlands).

We obtained information on species' migratory behaviour from Cramp and Perrins (1993) and used it to group species into migrant or resident species (variable migration) categories (Table 2). Migrant corresponds to long-distance migrants (trans-Saharan) while resident corresponds to species wintering in Europe (residents and short-distance migrants, intra Europe).

We estimated species' latitudinal preferences following Prodon (1993) (Table 2) and used it as an estimator of species' association to the Mediterranean region (variable latitude).

Second, to test whether the initial landscape had an effect on the strength of bird species' response to change, we classified the study sites into three categories according to their initial landscape (>50% crops or grasslands = farmland, >70% woodland or shrubs = woodland, others = mixed, Table 1).

3. Results

We obtained 410 effect sizes from 73 species representative of the bird communities of Mediterranean agro-forest systems (Table 2). The time period covered, the surface examined by the study and the study sample size had no effect on the bird species trends measured in the different studies (Table 3).

Overall, the mean effect size for all species was significantly positive (Table 4). Species' habitat preference had a significant effect on effect size (Table 3). Mean effect size in woodland species was significantly positive (based on 95% CI; Table 4) and significantly higher ($P = 0.011$) than mean effect size in farmland species, which did not differ significantly from zero (based on 95% CI; Table 4, and Fig. 2). Mean effect size was intermediate in shrubland species. Species' habitat breadth had a significant effect when all species were considered, and when only shrubland, farmland species or migrants were considered (Table 3): effect size increased significantly with species' habitat breadth (Table 4). Species' migratory status had a highly significant effect on the changes in occurrence of bird species (Table 3). Migrant species had a significantly lower mean effect size than resident species, both when considering all species and when species were categorized by habitat preferences (Table 4, and Fig. 3). Residents had a positive mean effect size that differed significantly from zero, both when all species were considered and when species were categorized by habitat association (based on 95% CI; Table 4). Migrants had a mean negative effect size that differed significantly from zero when all species were considered, and when only farmland species were considered. Species' latitudinal preferences had a significant effect on species' response to land abandonment when considering either all species, only shrubland species, farmland species or only residents (Table 3): effect size increased significantly with species' latitudinal preference (Table 4).

The nature of the initial landscape had a highly significant effect on effect sizes (Table 3). Mean effect size was lowest when the study site was in a landscape initially dominated by farmland, higher when the initial landscape was dominated by woodlands and even higher when the initial landscape was a mixture of both habitat types (Table 4, and Fig. 4). These effects of the initial landscape on mean effect size remained significant when species were categorized by habitat preference (Table 3, and Fig. 4), and relative differences between habitat types remained similar (Table 4). When the initial landscape was mixed, there was a significant positive mean effect size in all three species groups (based on 95% CI; Table 4).

4. Discussion

These results confirm the hypothesis that recent land abandonment has had a significant impact on bird community patterns in the north-western Mediterranean region, as has already been shown at a more local scale by a number of studies (e.g. Preiss et al., 1997; Coreau and Martin, 2007; Sirami et al., 2007). Our results are contrary to those expected from climate warming (i.e. predicted decrease of central European species and increase of Mediterranean species) and therefore support the hypothesis that land use change, such as land abandonment, is the main cause of recent changes in bird populations in the Mediterranean region.

The overall positive effect of land abandonment on species occurrences masks complex patterns of temporal changes in responses at the species level. Habitat selection corresponds to a first triage in species' response patterns, with woodland species benefiting most and farmland species being least favoured, in line with the broad patterns depicted by Birds in Europe (BirdLife International, 2004). As we used a simplified classification of species' habitat preference, which considerably increased the overlap between the different habitat categories (47% of the effect sizes corresponded to bird species associated with two or three habitats), we expect this analysis of the effect of habitat preference to be conservative. Beyond this expected result, changes in species occurrence seemed to result from a combination of biological attributes that make particular species more or less sensitive to land abandonment, and thus cause their occurrence to vary positively, negatively or not at all with land abandonment. Our results confirm that habitat breadth is a key attribute to understand response variability within species with the same habitat preferences (e.g. Swihart et al., 2003; Julliard et al., 2004), for example between farmland specialists that have decreased (e.g. *Lanius senator*) and generalists found in farmland that have increased over time (e.g. *Lullula arborea*; see Table 2 for more examples).

The results showed that sustained and often severe population declines observed for migrants over the last 30 years at the European scale (Sanderson et al., 2006) also affected bird communities from the north-western Mediterranean. Contrary to the "unique cause" hypotheses suggested by many authors (e.g. wintering conditions, Böhning-Gaese and Bauer, 1996; climate change, Archaux, 2002), our results suggest an "additive effect" of migration strategy and habitat selection, with migrant farmland species being the most negatively affected and resident woodland species benefiting the most

Table 2 – Bird species ordered by increasing value of effect size obtained for the multi-site analysis

Species	Habitat preference	Habitat breadth	Migration strategy	MLAT	Mean Multi-site effect size
Oenanthe oenanthe	Farmland	0.26	Migrant	56	−0.3704
Sylvia conspicillata	Shrubland	0.31	Migrant	36	−0.3206
Clamator glandarius	Farmland	0.47	Migrant	19	−0.2834
Oenanthe hispanica	Farmland/shrubland	0.20	Migrant	38	−0.2821
Lanius senator	Farmland/shrubland	0.27	Migrant	41	−0.2803
Garrulus glandarius	Woodland	0.52	Resident	47	−0.2307
Calandrella brachydactyla[*]	Shrubland	0.43	Migrant	41	−0.2060
Pyrrhula pyrrhula	Woodland	0.44	Resident	57	−0.1863
Emberiza citrinella	Farmland	0.43	Resident	56	−0.1512
Muscicapa striata	Woodland	0.48	Migrant	50	−0.1449
Luscinia megarhynchos	Woodland/shrubland	0.54	Migrant	42	−0.1261
Alauda arvensis	Farmland	0.59	Resident	53	−0.1207
Upupa epops	Farmland	0.47	Migrant	33	−0.1193
Alectoris rufa	Farmland/shrubland	0.42	Resident	42	−0.1096
Merops apiaster	Farmland/shrubland	0.45	Migrant	41	−0.1096
Coturnix coturnix	Woodland/farmland	0.59	Migrant	45	−0.0983
Motacilla alba	Farmland	0.58	Resident	52	−0.0871
Sylvia communis	Farmland	0.59	Migrant	50	−0.0788
Galerida cristata	Farmland/shrubland	0.44	Resident	37	−0.0699
Troglodytes troglodytes	Woodland	0.54	Resident	46	−0.0636
Streptopelia turtur	Woodland	0.51	Migrant	44	−0.0579
Emberiza cia	Shrubland	0.47	Resident	40	−0.0510
Anthus campestris[*]	Farmland/shrubland	0.62	Migrant	45	−0.0451
Petronia petronia	Woodland/shrubland	0.57	Resident	40	−0.0395
Loxia curvirostra	Woodland	0.48	Resident	54	−0.0316
Turdus viscivorus	Farmland	0.66	Resident	50	−0.0255
Emberiza hortulana[*]	Woodland/shrubland/farmland	0.71	Migrant	49	−0.0230
Sylvia borin	Woodland	0.50	Migrant	54	−0.0162
Oriolus oriolus	Woodland	0.50	Migrant	43	−0.0113
Serinus serinus	Woodland/shrubland	0.47	Resident	44	−0.0004
Carduelis carduelis	Farmland/shrubland	0.44	Resident	47	0.0002
Sylvia undata[*]	Shrubland	0.63	Resident	41	0.0037
Picus viridis	Woodland/farmland	0.62	Resident	50	0.0093
Jynx torquilla	Woodland	0.60	Migrant	53	0.0111
Phylloscopus bonelli	Woodland/shrubland	0.51	Migrant	42	0.0126
Aegithalos caudatus	Woodland	0.50	Resident	51	0.0139
Miliaria calandra	Farmland	0.51	Resident	42	0.0159
Prunella modularis	Woodland	0.41	Resident	53	0.0171
Carduelis chloris	Woodland/shrubland/farmland	0.44	Resident	49	0.0207
Parus caeruleus	Woodland	0.50	Resident	48	0.0431
Columba palumbus	Farmland	0.54	Resident	47	0.0432
Lanius collurio[*]	Woodland/shrubland/farmland	0.36	Migrant	48	0.0498
Carduelis cannabina	Woodland/shrubland/farmland	0.67	Resident	48	0.0526
Turdus merula	Woodland/shrubland/farmland	0.56	Resident	44	0.0581
Anthus trivialis	Woodland	0.44	Migrant	50	0.0615
Parus major	Woodland/farmland	0.58	Resident	45	0.0672
Sylvia hortensis	Woodland/shrubland	0.68	Migrant	38	0.0700
Corvus corone	Farmland	0.49	Resident	53	0.0747
Regulus regulus	Woodland	0.37	Resident	49	0.0761
Emberiza cirlus	Woodland/shrubland/farmland	0.53	Resident	40	0.0833
Saxicola torquata	Woodland/shrubland/farmland	0.52	Resident	46	0.1028
Cuculus canorus	Woodland/farmland	0.44	Migrant	50	0.1069
Dendrocopos major	Woodland	0.51	Resident	52	0.1079
Serinus citrinella	Woodland/shrubland	0.38	Resident	45	0.1087
Certhia brachydactyla	Woodland	0.50	Resident	44	0.1131
Sylvia cantillans	Shrubland	0.53	Migrant	38	0.1302
Hippolais polyglotta	Woodland/shrubland	0.50	Migrant	41	0.1357
Parus cristatus	Woodland	0.63	Resident	55	0.1394
Parus ater	Woodland	0.55	Resident	51	0.1566
Parus palustris	Woodland	0.40	Resident	48	0.1589
Sylvia melanocephala	Woodland/shrubland	0.46	Resident	37	0.1691
Fringilla coelebs	Woodland/shrubland	0.52	Resident	51	0.2101
Regulus ignicapilla	Woodland	0.52	Resident	44	0.2153
Sylvia atricapilla	Woodland	0.50	Resident	51	0.2195

(continued on next page)

Table 2 (*continued*)

Species	Habitat preference	Habitat breadth	Migration strategy	MLAT	Mean Multi-site effect size
Erithacus rubecula	Woodland/shrubland/farmland	0.56	Resident	52	0.2403
Lullula arborea*	Woodland/shrubland/farmland	0.67	Resident	47	0.2438
Sitta europaea	Woodland	0.51	Resident	53	0.3099
Galerida theklae*	Shrubland	0.30	Resident	28	0.3345
Melanocorypha calandra*	Farmland	0.29	Resident	41	0.3410
Phylloscopus collybita	Woodland	0.46	Resident	57	0.3603
Turdus philomelos	Woodland/farmland	0.50	Resident	55	0.3760
Dryocopus martius*	Woodland	0.43	Resident	56	0.4077
Dendrocopos minor	Woodland	0.41	Resident	55	0.4165

Habitat preference, main habitat(s) associated to each species (from (Tucker and Evans, 1997) ("farmland" refers to both cultivated and grazed open habitats; "shrubland" refers to open to closed shrublands and "woodland" refers to open woodlands to closed forests), habitat breadth, value estimated from Catalan Breeding Bird Atlas (Estrada et al., 2004); Migration strategy, migrant or resident; latitude, mean latitude (from Prodon, 1993); multi-site effect size, effect size calculated for the eight sites. Stars (*) indicate bird species with special protection status in the European Union (listed on Annex I of the EU Wild Birds Directive).

Table 3 – Results of random effect meta-analytic models assessing the role of habitat preference (woodland, shrubland, and farmland) and then the role of four covariates for all species and for the three subsets defined according to species habitat preference: migration (migrant versus resident), latitude (continuous), habitat breadth (continuous), landscape (woodland, farmland, mixture)

	df	Q	P
Time period	2	1.94	0.380
Area	2	1.72	0.423
Sample size	2	5.97	0.051
Habitat preference			
All species	2	6.72	**0.035**
Habitat breadth			
All species	1	7.02	**0.008**
Woodland	1	0.16	0.691
Shrubland	1	5.03	**0.025**
Farmland	1	6.61	**0.010**
Migrants	1	6.83	**0.009**
Residents	1	0.10	0.460
Migration			
All species	1	27.96	<**0.001**
Woodland	1	8.91	**0.003**
Shrubland	1	7.47	**0.006**
Farmland	1	11.59	**0.001**
Latitude			
All species	1	16.56	<**0.001**
Woodland	1	7.06	**0.008**
Shrubland	1	2.51	0.113
Farmland	1	5.64	**0.018**
Migrants	1	1.28	0.258
Residents	1	6.34	**0.012**
Landscape			
All species	2	26.83	<**0.001**
Woodland	2	11.06	**0.004**
Shrubland	2	14.81	**0.001**
Farmland	2	6.23	**0.044**
Migrants	2	21.82	<**0.001**
Residents	2	14.39	**0.001**

The variable Q is the chi-square value of the test for homogeneity used to judge significance (P values) according to the degrees of freedom (df) of the test. Bold P values are significant at $P < 0.05$.

from land abandonment. Recent studies have suggested that migrants may be less adaptable to changes in resource availability (Sol et al., 2005), perhaps due to small relative brain size and high resource specialization (Shultz et al., 2005). The strong effect of habitat breadth observed for migrants in our study may support this hypothesis. In parallel, the strong effect of species' latitudinal distribution for residents could be linked to the greater sensitivity to habitat loss and

Table 4 – Mean effect sizes by group (for categorical covariates) and slopes of the regression (for continuous covariates) derived from random factor meta-analytic models on all species and on the three subsets defined according to species habitat preference

		All species	Woodland species	Shrubland species	Farmland species	Migrants	Residents
Mean effect size	Overall	0.05 ± 0.02	0.08 ± 0.03	0.04 ± 0.05	0.01 ± 0.04	–	–
	Migrants	−0.05 ± 0.04	0.01 ± 0.10	−0.04 ± 0.08	−0.11 ± 0.08	–	–
	Residents	0.09 ± 0.03	0.11 ± 0.04	0.09 ± 0.06	0.05 ± 0.05	–	–
	Farmland landscape	−0.01 ± 0.04	0.01 ± 0.05	−0.02 ± 0.07	−0.03 ± 0.06	−0.11 ± 0.06	0.03 ± 0.04
	Woodland landscape	0.06 ± 0.04	0.11 ± 0.06	0.02 ± 0.08	−0.01 ± 0.08	−0.09 ± 0.07	0.11 ± 0.04
	Mixed landscape	0.15 ± 0.057	0.15 ± 0.08	0.20 ± 0.09	0.11 ± 0.09	0.13 ± 0.09	0.16 ± 0.06
Slope	H. breadth	0.37 ± 0.14	−0.11 ± 0.29	0.52 ± 0.23	0.55 ± 0.21	0.53 ± 0.20	0.03 ± 0.19
	Latitude	0.0085 ± 0.0021	0.0096 ± 0.0036	0.0076 ± 0.0048	0.0083 ± 0.0035	0.0042 ± 0.0038	0.0067 ± 0.0026

Mean effect size values are weighted means ±95% confidence interval. Slope values are values ± SE.

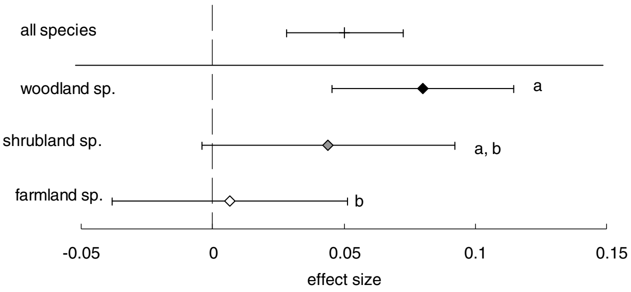

Fig. 2 – Overall effect size and effect of bird species habitat preference on effect size (mean effect size ±95% confidence interval (CI) for all species, for woodland species in black, shrubland species in grey and farmland in white; values with identical letters do not differ significantly).

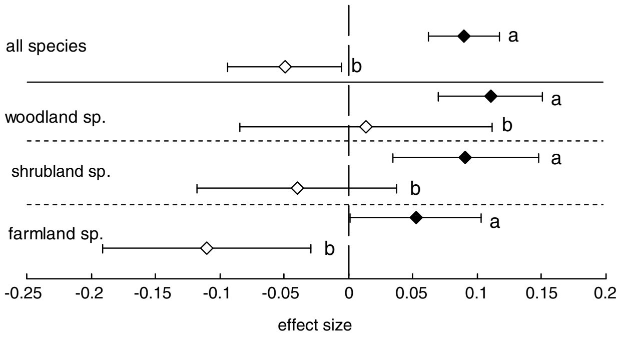

Fig. 3 – Effect of migratory behaviour on bird species effect size for all species and for the three subsets of species categorized by habitat preference: woodland species, shrubland species and farmland species (mean effect size ±95% CI for resident in black and migrant in white; for each subset, values with identical letters do not differ significantly).

fragmentation of bird species occurring at the periphery of their geographical range, especially at northern margins (Swihart et al., 2006).

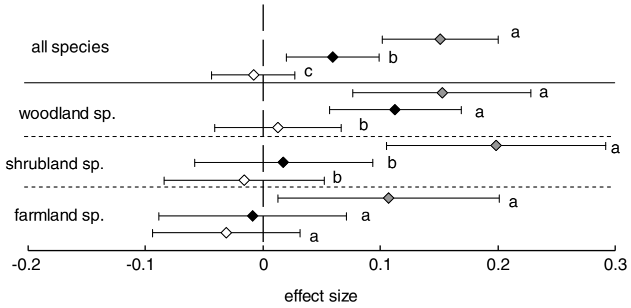

Fig. 4 – Landscape effect on long-term occurrence changes for all bird species and for the three subsets of species categorized by habitat preference: woodland species, shrubland species and farmland species (mean effect size ±95% CI for mixed landscape in grey, woodland landscape in black and farmland landscape in white; for each subset, values with identical letters do not differ significantly).

The general positive effect of land abandonment on species occurrence observed over the eight study sites masked a strong variability in bird species' response among landscape types. The weak impact of land abandonment on species occurrence in landscapes initially dominated by farmland might result from insufficient vegetation changes due to slow establishment of woody plants in a landscape dominated by farmland (Debussche and Lepart, 1992). In initially forested landscapes, the positive impact of land abandonment was slightly more pronounced than in landscapes initially dominated by farmland, probably because of the lower occurrence of farmland species with smaller potential for further decreases. However, the impact was less pronounced than in initially mixed landscapes, probably due to a limited response of shrubland species resulting from the small amount of the landscape susceptible to becoming shrubland through vegetation succession. The highest effect of land abandonment in initially mixed landscapes could result from two processes acting simultaneously: first, the higher rate of conversion of habitats in heterogeneous landscape (Debussche and Lepart, 1992), together with a potential for rapid response of woodland and shrubland bird metapopulations (Opdam et al., 2001); and second, the differences in farmland species' composition between landscape types. Indeed, 30% of the farmland species found in the farmland-dominated landscapes were specialists (e.g. *Oenanthe oenanthe*), whereas the farmland species associated with initially mixed landscapes were mainly ecotone species, linked to two or more coexisting habitat types (e.g. *Lullula arborea*). Such species can be expected to benefit from an increase in landscape heterogeneity (Benton et al., 2003; Brotons et al., 2004). The analysis of the importance of the landscape type in explaining the effect of land abandonment on bird species occurrence suggests the existence of three distinct steps in the long-term processes that are currently taking place in the Mediterranean region. First, as succession causes previously farmed and grazed habitats to turn into scrub, abandonment triggers an impoverishment of the bird communities through the loss of the most typical farmland/open habitat species. Second, as the scrub matures into early stage woodlands, there is a temporary increase in the broad suite of species, ranging from farmland generalists and shrubland species to woodland generalists. Third, as the woodland matures and expands, the bird community becomes simplified and dominated by woodland specialists after the loss of shrubland and ecotone species.

5. Conclusions and conservation implications

Current bird community patterns in the Mediterranean region seem to be affected more by large-scale habitat changes, such as land abandonment and intensification, than by climate change. Declining species in our study are those typical of Mediterranean landscapes, often with a high conservation status (e.g. *Calandrella brachydactyla*, *Anthus campestris*, and *Emberiza hortulana*), whereas increasing species are common Eurasian species (e.g. *Turdus philomelos* and *Phylloscopus collybita*). The dramatic impact of land use changes would be even more striking if the concomitant impact of intensification had been considered. The latter has negatively affected some Mediterranean farmland species (e.g. *Calandrella brachydactyla* in north-eastern Spain), while some other species have been affected by both agricultural intensification *and* abandonment (e.g. *Falco naumanni*; Tella et al., 1998). Whilst our results indicate that land abandonment is a real threat to some species in certain areas, it is important to note that our meta-analysis did not cover many species typical of Mediterranean steppes, due to dataset selection constraints. The last Spanish steppes hold the most habitat-restricted, often Mediterranean endemic and endangered species (e.g. Dupont's Lark *Chersophilus duponti*), for which land abandonment designed to restore natural, steppe vegetation may be the most effective way to recover both the habitat and bird populations (e.g. Laiolo and Tella, 2006).

Beyond this, our results suggest a need to integrate the role of several biological attributes, such as migration strategy and habitat breadth, in order to gain a more detailed understanding of the dynamics triggered by abandonment and an improved predictive power. Better predictions about bird species' responses to change should help improve the design of management strategies. Our results also emphasize the need to better understand the combined effects of constraints imposed by migratory behaviour and their interaction with those stemming from land use changes. Only three of the species declining in the present study are included on Annex I of the EU Wild Birds Directive (*Calandrella brachydactyla*, *Anthus campestris* and *Emberiza hortulana*), all of which are migrants. In contrast, the six other species listed on Annex I and covered by this study all increased, and five of these are residents. Of the 30 declining species, 57% are migrants and 50% are considered to be in unfavourable conservation status in Europe, whereas 81% of the 43 increasing species are residents and 70% are considered to be in favourable conservation status in Europe (BirdLife International, 2004). This underlines the need for more research on declining migrants, not only on their breeding grounds, but also on their migration routes and wintering grounds, to inform conservation needs and improve their fortunes in the Mediterranean and beyond.

In order to confirm the generality of our findings, more local scale, long-term studies that cover a broader range of Mediterranean countries and situations (e.g. intensification and land abandonment in the steppes) are badly needed, including improved bird monitoring schemes at local, regional and national scales. In Birds in Europe, the poor quality of the bird population trend data available from the Mediterranean contrasts with the high quality of such data in the rest of Western Europe (BirdLife International, 2004). All together, increasing knowledge on regional trends and integrating biological attributes should improve our ability to develop scenarios of biodiversity change and to elaborate better conservation policies at appropriate scales.

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