

Bird species in Mediterranean pine plantations exhibit different characteristics to those in natural reforested woodlands

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Abstract Passive woodland regeneration following cropland abandonment and pine plantations are two major approaches for vegetation restoration in agricultural landscapes in the Mediterranean Basin. We compared the effects of these two contrasting approaches on local bird density in central Spain on the basis of species characteristics, including regional density, habitat breadth, life-history traits and plumage colouration. Local bird density increased with regional density and habitat breadth in both woodland and pine plantation plots following macroecological patterns of bird abundance and distribution. In woodlands, dichromatic species were more abundant than monochromatic species and bird density increased with the intensity of territory defense and as the proportion of plumage colour generated by pheomelanin decreased. Contrary to our prediction, this latter observation suggests that woodlands may induce higher levels of physiological stress in birds than pine plantations even though these represent a novel habitat change. In pine plantations, sedentary species were more abundant than migratory species

and bird density was negatively related to body and egg mass. These traits of bird species in pine plantations are characteristic of successful invaders. The variation in bird density explained by phylogeny was twice as high in pine plantations as in woodlands, suggesting that pine plantations limit accessibility to some clades. Our results support, from an evolutionary perspective, the described inability of pine plantations on cropland to maintain or increase bird diversity in Mediterranean agricultural landscapes.

Keywords Habitat restoration · Life history · Pheomelanin · Plumage colouration · Vegetation restoration

Introduction

In the last few decades, large tracts of cropland in the world have been abandoned or reforested, resulting in noticeable effects on biological communities (Laiolo et al. 2004; Rey Benayas et al. 2007). Cropland abandonment can lead to secondary succession (Rey Benayas et al. 2008), which may take several decades in low-productivity environments such as Mediterranean areas (Bonet and Pausas 2004). Cropland reforestation has been proposed to produce forest land over a shorter timescale than that at which secondary succession occurs naturally. In the case of the Agrarian Common Policy scheme of the European Union, this has been done through tree plantations focused on pine species (Meijl et al. 2006). Reforestation with pines creates a vegetation structure that is different from that present in natural Mediterranean woodlands. Thus, natural Mediterranean woodlands present higher tree cover and less complexity of vegetation strata than pine plantations (Siri et al. 2007; Rey Benayas et al. 2010), hence the

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impacts of these plantations on biodiversity (Donald 2004). Therefore, pine plantations in croplands represent novel environments to be colonised by native wildlife.

Birds represent the group of vertebrates upon which the effects of vegetation change in Mediterranean areas have been most intensively studied (Díaz et al. 1998; Santos et al. 2002; Suárez-Seoane et al. 2002; Tellería et al. 2003; Sirami et al. 2007, 2008a, b). These studies have focused on community-level effects. However, the autoecological characteristics of bird species that colonise newly forested habitats have received less attention, although the capacity of species to respond to changing landscapes has been recognised to be a crucial factor driving community dynamics (Sirami et al. 2008a). Habitat requirements are the autoecological features most often used to explain the success of bird species in colonising reforested systems in Mediterranean areas, as increases in tree canopy cover favour woodland species and trigger shrubland species that are characteristic of Mediterranean native habitats (Díaz et al. 1998; Suárez-Seoane et al. 2002; Sirami et al. 2008a, b). If pine plantations in croplands represent novel environments for native Mediterranean birds, the autoecological characteristics of species that inhabit them should be similar to those of successfully colonising or invading species. Additionally, these characteristics may explain the success of birds in pine plantations. To our knowledge, a possible similarity between species colonising afforested habitats and invasive species has never been tested.

Different traits predict the colonisation success of birds; the most important of these are migratory strategy (Veltman et al. 1996; Sol and Lefebvre 2000; Sol et al. 2005), body mass (Veltman et al. 1996; Green 1997; Sol and Lefebvre 2000; Blackburn and Duncan 2001; Sol et al. 2002; Cassey 2001), relative brain mass (Sol and Lefebvre 2000; Sol et al. 2002, 2005), clutch size (Veltman et al. 1996; Green 1997; Cassey 2001; Duncan et al. 2001) and sexual plumage dichromatism (Sorci et al. 1998; McLain et al. 1999). The size of the natural range of the species also plays a role in the case of spontaneous (i.e. not facilitated by human interventions) invasions (Crocì et al. 2007; Møller 2009). Therefore, bird species colonising pine plantations in Mediterranean areas should present the characteristics of invasive species overall (see specific predictions below). Here, we test this hypothesis by comparing species characteristics that predict bird abundance in two scenarios that represent contrasting approaches for vegetation restoration in abandoned cropland in Mediterranean landscapes, namely secondary succession and active vegetation restoration. With this aim, we surveyed bird species in stands under secondary succession (referred to as woodlands hereafter) or planted with coniferous trees (referred to as pine plantations hereafter) in central Spain, where these two contrasting trajectories of vegetation

restoration deviate from recently (<60 years, mostly <15 years) abandoned cropland.

We made the following predictions (Table 1). (1) Species that are sedentary, have a small body mass and a large clutch size should be more abundant than species with the opposite characteristics in pine plantations, as these are characteristics of species with high rates of population growth and are thus expected to have greater establishment success in novel environments (Duncan et al. 2003). Although species with high population growth rates also tend to have more variable population sizes, which could increase their risk of extinction in novel environments (Duncan et al. 2003; Schaffner 2005), small body size is a predictor of establishment success across species (Cassey 2001). As egg mass covaries with body mass across species (Sæther 1987; Poiani and Jermiin 1994), the same was predicted for egg mass. (2) Large relative brain mass should be a predictor of species density in pine plantations, as this trait reflects behavioural flexibility (Sol and Lefebvre 2000) and, more specifically, the diversity of food type and technical innovations of species (Overington et al. 2009). (3) Sexually monochromatic species should be more abundant than dichromatic species in pine plantations, as the conspicuous colourations displayed by the latter reduce their capacity to adapt to novel environments due to predation vulnerability and an increased risk of extinction (Sorci et al. 1998; Møller and Nielsen 2006). (4) Bird species that do not defend territories during the breeding season should be more abundant in pine plantations than territorial species, as absence of territoriality is related to high population growth in animals and particularly in birds (López-Sepulcre and Kokko 2005). Similarly, absence of territoriality has been found to be related to high invasion success by birds in novel environments produced by urbanisation (Blair and Johnson 2008). By contrast, territorial species should be more abundant in woodlands (Blair and Johnson 2008). We tested all of these predictions while controlling for the effect of maximum observed density at a regional scale, as this variable should be positively related to the density of species in both contrasting vegetation restoration trajectories. Similarly, we controlled for the effect of regional habitat breadth (Crocì et al. 2007), as high habitat breadth is indicative of common species that tolerate a wide range of ecological conditions (Carrascal and Seoane 2008).

In addition, we tested if bird species density in the two contrasting vegetation restoration trajectories is differentially predicted by the extension of melanin-based plumage colouration. The expression of plumage colour generated by melanins is intrinsically related to oxidative stress (i.e. the imbalance between the production of reactive oxygen species and the state of the antioxidant and repair machinery; Galván and Alonso-Alvarez 2008, 2009;

Table 1 Predictions made for bird species density in two contrasting trajectories of vegetation restoration in agricultural landscapes of Central Spain regarding ecological, life-history and morphological traits, and results obtained in the present study considering that the most abundant bird species establishing in a novel habitat type (i.e. pine plantations) should exhibit the characteristics of good invaders

Predictor variable	Prediction for passive restoration (secondary succession)	Prediction confirmed	Prediction for active restoration (pine plantations)	Prediction confirmed
Regional population effects				
Maximum regional density	+	Yes	+	Yes
Regional habitat breadth	+	Yes ^a	+	Yes ^a
Life-history traits				
Sedentariness	No effect	Yes	+	Yes
Territoriality	+	Yes	–	Yes ^a
Clutch size	No effect	Yes	+	No
Egg mass	No effect	Yes	–	Yes
Morphology and colouration				
Body mass	No effect	Yes	–	Yes
Relative brain mass	No effect	Yes	+	No
Sexual dichromatism	No effect	No	–	No
Eumelanic plumage score	No effect	In the other restoration trajectory	+	In the other restoration trajectory
Pheomelanic plumage score	No effect	In the other restoration trajectory	–	In the other restoration trajectory

“+” and “–” indicate that the effect on bird density should be positive and negative, respectively

^a Means that the result was in the predicted direction, but that the magnitude of the effect was lower than for other factors as deduced from the PLSR models (see Table 2)

Galván and Solano 2009), and novel habitat changes such as pine plantations can cause physiological stress (i.e. physiological, hormonal or behavioural changes that occur as a response to unpredictable and noxious stimuli; sensu Romero 2004) in birds (Badyaev 2005), which in turn can induce oxidative stress (e.g. Lin et al. 2004). Thus, melanisation levels of birds may predict their abundance in the contrasting trajectories of vegetation restoration. The extension of plumage colour generated by eumelanin (i.e. the darkest form of melanin) may predict species density in pine plantations because the production of this pigment proceeds under high levels of endogenous oxidative stress, which would increase the tolerance to stress of these species (Galván and Alonso-Alvarez 2009; Galván and Solano 2009). By contrast, the production of pheomelanin (i.e. the lightest form of melanin) requires higher levels of antioxidants to proceed (Galván and Alonso-Alvarez 2009; Galván and Solano 2009), so species with a high proportion of pheomelanin-based plumage colour may be more limited when establishing in pine plantations (Table 1; see also Møller et al. 2010 for similar predictions for access to dietary antioxidants). The results of this investigation will provide useful insights for explaining what kind of species from the available species pool is attracted by

active restoration plots (Haila and Järvinen 1983), as well as mechanistic patterns of colonisation of novel habitats by birds that are expanding in many regions across the world.

Materials and methods

Study area

We surveyed bird communities in a ca. 6,000 km² area of the Mesomediterranean bioclimatic domain (Rivas-Martínez 1981) located in central Spain. Extreme coordinates for the area are 41°00'N (north), 39°54'N (south), 3°46'W (west) and 2°51'E (east). Altitude ranges between 631 and 1,008 m a.s.l. Climate in this region is continental Mediterranean, with cold winters and warm dry summers.

Natural vegetation chiefly consists of evergreen forests dominated by holm oak *Quercus rotundifolia*. The degradation of these forests has led to more open woodland dominated by *Q. ilex*, *Q. coccifera* or *Juniperus oxycedrus*, or to shrubland dominated by *Cistus ladanifer*, *Retama sphaerocarpa*, camephytes such as *Thymus* and *Lavandula* species, and herbs (e.g. *Stipa* spp.). Large tracts of land

were reforested with pine species (*Pinus halepensis* and *P. pinea*) after the 1950s and the oldest pine plantations are now considered semi-natural forests (Peñuelas and Ocaña 1996). Following subsidies from the European Union, some cropland area was planted almost entirely with *P. halepensis* after 1993. Thus, most of the afforested abandoned cropland ranged between 3 and 15 years of age at the time that we surveyed the bird communities. The natural or semi-natural vegetation and pine plantations intermingle with farmland, which mostly consists of rain-fed cereals and recently abandoned (<4 years old) cropland under secondary succession.

Bird censuses

We carried out bird censuses during the breeding seasons (28 April and 1 June) of two consecutive years (2008–2009) by means of single-visit point counts (Bibby et al. 2000), each 10 min long, during which all birds heard or seen within a 50-m radius plot were recorded. We did not consider overflying birds. The censuses were conducted by the same two well-trained field technicians on windless and rainless days between sunrise and 1100 hours GMT in the morning. Point counts do not provide absolute densities but relative abundances. Nevertheless, the small area covered by the plots (0.78 ha) and the relatively long time devoted to bird counts maximise the detection probability of species and, thus, the accuracy of estimations of their abundance (Shiu and Lee 2003). Bird censuses were conducted in pine plantations and natural woodlands, as well as in recently abandoned crops (<4 years old) surrounding them, because they contain species that could potentially occupy pine plantations and natural woodlands. We detected a total of 44 bird species [“Electronic supplementary material” (ESM) resource 1]. From these, two were present in neither pine plantations nor natural woodlands and were only detected in croplands (i.e. the common skylark *Alauda arvensis* and the common quail *Coturnix coturnix*; see ESM resource 1). These two species were nevertheless included in the analyses because they can potentially occupy pine plantations and natural woodlands. The remaining species were present in pine plantations and/or natural woodlands.

Prior to sampling, we first explored the entire territory by means of aerial photographs and Google Earth, and then visited the potential survey localities in order to locate the census plots. A total number of 152 census plots were obtained in 48 localities distributed throughout the study area in an attempt to sample the whole range of habitats present and the full gradient of altitudes. Each plot was only censused during one of the two years, but the censusing was organised such that each habitat was censused on both years. We did not observe any clear interannual

variation in bird abundance of the study species, so we pooled all the censuses obtained in both years. We georeferenced the census plots with a portable GPS and interspersed these so that they were at least 200 m from each other. We selected plots that included the dominant habitat types of the study area. These main habitat types were abandoned cropland, pastureland, camephyte shrubland, shrubland (mainly of the genera *Cistus* and *Genista*), several stages of holm oak succession to mature stands, and a range of afforested croplands with pines (from seedlings to pine stands ca. 60 years old). We used these habitat types as guidelines to select the survey localities. Of the 152 plots, 62 were located in stands under woodland secondary succession, 75 in pine plantation stands, and 15 in recently (<4 years) abandoned cropland stands. A full description of the habitat features of the census plots can be found in Rey Benayas et al. (2010).

Bird regional density and habitat breadth

We summarised regional patterns of distribution–abundance for the bird species detected in the 152 point counts according to maximum density and habitat breadth of species in the biogeographic region that included the study area (Central Spain, Mesomediterranean region). We estimated the maximum regional density (birds/km²) recorded in 13 major habitat types of the study region as a measure of the maximum ecological abundance that a species can attain in its most favourable environment. We established these 13 habitat types considering vegetation structure, floristic composition and human impact, and these habitat types accounted for more than 95% of the surface of the whole study area. They were the following: two types of urban environment (that differed in terms of building height and density), nonirrigated arable crops, irrigated arable crops, mixed orchards, vineyards, olive plantations, two types of shrubland (according to shrub height and density), pasturelands, pinewoods, deciduous woodlands and holm oak woodlands. We obtained the database for this analysis from the Spanish SACRE program (which monitors common breeding birds in Spain), using 3,417 five-min point counts performed in 2004–2006 and distributed over the study area. We obtained absolute densities for this database using the detectability provided by Carrascal and Palomino (2008) for the same census program.

We calculated regional habitat breadth of species in the 13 major habitat types following Levins' (1968) index divided by the number of habitat categories:

$$HB = [(\sum p_i^2)^{-1}]/13,$$

where p_i is the proportion of the density for each species measured in the habitat i (dividing the density in habitat i by the sum of all maximum densities recorded in the 13

habitat types). This index ranges between 1 (evenly distributed across the 13 habitat types) and 1/13 (only present in one habitat type).

Morphological and life-history traits of birds

We obtained body masses and brain masses of the bird species detected in the census plots from Mlikovsky (1989), Møller et al. (2005, 2006), Garamszegi et al. (2007a, b) and Møller (2008). Highly significant repeatabilities among studies indicate that information on brain mass can be combined across sources (Garamszegi et al. 2005). We calculated relative brain mass as the residuals of the log–log regression of brain mass against body mass. We obtained body mass from the same source as brain mass, but when brain mass was not available (six species; ESM resource 1), we took body mass from Lislevand et al. (2007).

We took information on clutch size, egg mass and territorial behaviour from Lislevand et al. (2007). We defined territorial behaviour by a three-level variable: score 0: species in which males and females do not share resources and feed away from their breeding territory; score 1: species in which males and females share resources on their territory only during the breeding season; score 2: species in which males and females share resources on their territory all year round (Lislevand et al. 2007). These scores were consistent among observers ($r_s = 0.628–0.674$, $n = 1454–1629$ species, $P < 0.001$; Lislevand et al. 2007). Territorial behaviour was not available for five species (ESM resource 1). We took information on the migratory strategies of birds (trans-Saharan migrant, score 0 vs. resident, score 1) in the study area from Seoane and Carrascal (2007).

Bird plumage colouration

We obtained information on sexual dichromatism in plumage by examining illustrations in Cramp and Simmons (1977–1994) and photographs of birds captured in Spain from the *Identification Atlas of Birds of Aragón* (Blasco Zumeta 2010). We also examined text descriptions of plumage characteristics in these sources. We considered that a species was sexually dichromatic (score 1) when both sexes exhibited a conspicuous and clearly distinguishable difference in plumage colouration. Otherwise the species were categorised as monochromatic (score 0). Seddon et al. (2010) have recently shown that human visual assessment of sexual dichromatism is positively correlated with the avian perception of the trait. Although species that we consider sexually monochromatic may indeed be dichromatic regarding ultraviolet (UV) reflectance, to which we are blind, UV reflectance is generated by structural feather colourations (Prum 2006). However, most

species in our list do not present such colourations; they are mainly coloured by melanins. Thus, it is unlikely that a classification of mono/dichromatic species that considers UV reflectance would significantly change our conclusions.

Eumelanic and pheomelanic traits are generally of distinctive colours, the former being responsible for black and grey colours and the latter for yellowish, reddish, chestnut and brown colours (Toral et al. 2008). Eumelanin and pheomelanin normally occur simultaneously in the tissues (Ozeki et al. 1997), but the fact that darker colours are conferred by eumelanin (Toral et al. 2008) indicate that there are lower contents of this pigment in chestnut and brown colours as compared to black and grey colours (Galván and Alonso-Alvarez 2009). Furthermore, many bird species present feather melanin contents of high purity (>90% of either eumelanin or pheomelanin; McGraw and Wakamatsu 2004; J.J. Negro personal communication). Therefore, we considered that black and grey plumage colours were predominantly generated by eumelanin, while chestnut and brown colours were predominantly generated by pheomelanin. We did not consider conspicuous yellow or red colourations that could have been generated by other pigments (i.e. carotenoids), unless they were chemically identified as melanin-based by Toral et al. (2008). Although only a rough approximation to the real proportions of eumelanic and pheomelanic plumage, the assumption that black-grey colours are eumelanic and that brown-chestnut colours are pheomelanic should be adequate for comparative purposes (Owens and Hartley 1998). Thus, one of us (IG) quantified the proportion of melanic plumage parts by examining illustrations in Cramp and Simmons (1977–1994) and photographs of birds captured in Spain in the *Identification Atlas of Birds of Aragón* (Blasco Zumeta 2010). Several authors have used this method previously (see, e.g., John 1995; Yezerinac and Weatherhead 1995; Caro 2009), and it has been shown to be a reliable method of quantifying different components of plumage colour that is even correlated with the avian perception of colour (del Val et al. 2009; Seddon et al. 2010). We examined illustrations of both resting and flying birds. We followed the method used by Beauchamp and Heeb (2001) and Galván (2008) to obtain estimates of the proportions of eu- and pheomelanic colours present in the plumage of each species, assigning scores that ranged from 0 (total lack of melanic colour) to 5 (all melanic). When a species was sexually dichromatic regarding the type of melanin-based colouration (i.e. eumelanic vs. pheomelanic), we averaged the eumelanic and pheomelanic scores obtained for males and females. Our scores were highly correlated with those assigned by an independent observer (eumelanin-based colour score: $r_s = 0.85$, $n = 44$ species, $P < 0.0001$; pheomelanin-based colour score: $r_s = 0.93$, $n = 44$ species, $P < 0.0001$).

Data analyses

We analysed the relationships between the response variables (average bird density in the two contrasting vegetation restoration trajectories) and ecological, morphological and life-history traits of the species (predictor variables) by means of partial least squares regressions (hereafter PLSR; Carrascal et al. 2009), using the species as the sample unit ($n = 44$). This statistical tool is an extension of multiple regression analysis where associations are established with factors extracted from predictor variables that maximise the explained variance in the dependent variable. These factors are defined as a linear combination of independent variables, so the original multidimensionality is reduced to a lower number of orthogonal factors to detect structure in the relationships between predictor variables and between these factors and the response variable. The extracted factors account for successively lower proportions of original variance. We calculated the relative contribution of each variable to the derived factors by means of the square of the predictor weight. Results obtained with PLSR are similar to those from conventional multiple regression techniques; however, this method is extremely robust to the effects of sample size and degree of correlation between predictor variables, which makes PLSR especially useful when the sample size is small and in cases of severe multicollinearity (Carrascal et al. 2009). We introduced all predictor variables as continuous variables (log-transformed) in the PLSR models, except migratory strategy and sexual dichromatism, which were introduced as categorical factors.

Bird species are evolutionarily related through phylogeny and thus should not be treated as independent sample units (Felsenstein 1985). Therefore, the effect of common ancestry among taxa can lead to an overestimation of degrees of freedom if phylogenetic relationships are not taken into account. We used phylogenetic eigenvector regression (PVR) to quantify the amount of phylogenetic signal and to correct for it in the analysis of the relationship between bird density and ecological, morphological and life-history traits (Diniz-Filho et al. 1998). Diniz-Filho and Torres (2002) and Martins et al. (2002) tested several comparative methods (Felsenstein's independent contrasts, autoregressive method, PVR, and phylogenetic generalised least squares) and found that PVR yields good statistical performance regardless of the details of the evolutionary mode used to generate the data, and provides similar results to other methods, with very good (i.e., low) type I and II errors. Moreover, PVR does not assume any evolutionary model a priori (an advantage if the true evolutionary model is unknown or if it is too complex), and it gives similar statistical performance even for evolutionary processes that are distinct from Brownian motion.

We took the phylogenetic hypothesis (ESM resource 2) from the species-level supertree constructed by Davis (2008). Since this supertree was not calibrated, as it was made from different phylogenies that used different methods, we set all branch lengths equal to unity in our compiled phylogeny, thus assuming a speciation model of evolution.

We first performed a principal coordinates analysis (PCORD) on the matrix of pairwise phylogenetic distances between the 44 bird species (after a double-centre transformation). In a second step we selected the first ten eigenvectors to account parsimoniously for the phylogenetic signal. Eigenvectors extracted from double-centred phylogenetic distance matrices are able to detect the main topological features of the cladogram under different sample sizes or numbers of taxa used in the analyses (Diniz-Filho et al. 1998). We found that the original matrix of phylogenetic distances between the 44 bird species and the reproduced matrix of distances estimated based on the first ten eigenvectors were very similar (Mantel test with 999 randomised matrices to estimate significance: $r = 0.920$, $P < 0.001$; test carried out using PopTools 3.1; Hood 2009). We used these eigenvectors as additional predictor variables in the PLSR models described above in order to control for phylogeny.

We used the Akaike information criterion (AIC) (Burnham and Anderson 2004) to corroborate the results obtained with the PLSR models. With this aim, we selected the most important predictor variables that resulted from the PLSR models (i.e. those with predictor weights that retained >5% of the information content of the PLSR axes) and developed a generalised linear model (GLM) for the dependent variables and these predictor variables. We calculated Akaike's second-order information criterion (AICc) and weights (w) for all possible models with these variables, considering that two models were equally probable if the difference in AICc (ΔAICc) or the quotient of their weights was >2 (Burnham and Anderson 2004). We carried out all analyses using MVSP version 3.13 (Covach Computing Services) and Statistica 8.0 (StatSoft Inc.).

Results

Bird density in woodlands

The PLSR model generated an axis that explained 22.1% of the variation in bird density in woodland plots. Bird density was significantly correlated with this axis (Table 2, Fig. 1). This PLSR component was positively related to maximum regional density, sexual dichromatism (i.e. dichromatic species were more abundant than

Table 2 Predictor weights of the two partial least squares regression (PLSR) analyses explaining the relationship between the average densities of 44 bird species occurring in 152 surveyed census plots (50 m radius; birds/10 ha) in two contrasting trajectories of vegetation restoration in agricultural landscapes of Central Spain (response variables) and the ecological, life-history and morphological traits of the species (predictor variables)

Predictor variable	Passive restoration (secondary succession)	Active restoration (pine plantations)
Regional population effects		
Maximum regional density (no. birds/10 ha)	0.33	0.45
Regional habitat breadth	0.15	0.22
Life-history traits		
Migratory strategy	0.19	0.27
Territoriality	0.40	-0.13
Clutch size	-0.04	-0.14
Egg mass (g)	-0.18	-0.31
Morphology and colouration		
Body mass (g)	-0.21	-0.25
Relative brain mass	0.22	-0.04
Sexual dichromatism	0.24	0.10
Eumelanic plumage colour score	0.21	-0.03
Pheomelanic plumage colour score	-0.34	0.12
Phylogenetic effects		
EV1	-0.24	0.18
EV2	-0.29	-0.03
EV3	-0.08	0.23
EV4	-0.12	-0.06
EV5	-0.01	0.20
EV6	-0.01	0.05
EV7	0.11	0.29
EV8	-0.12	-0.14
EV9	-0.01	0.26
EV10	0.20	0.25
% Variance accounted for	22.1	30.0
Eigenvalue	2.25	2.02

Additional predictor variables account for variability due to phylogenetic effects, which are computed from the first ten eigenvectors (EV1–EV10) obtained from a principal coordinates analysis applied to the matrix of pairwise phylogenetic distances between the 44 bird species. Predictor weights represent the contribution of each predictor variable to the PLSR axis. Predictor weights that retain >5% of the information content of the PLSR axis are shown in bold type

monochromatic species), and territorial behaviour (i.e. bird density increased with the intensity of territory defense) (Table 2, Fig. 2). By contrast, the PLSR component was negatively related to pheomelanic plumage colour score, indicating that the lower the proportion of plumage generated by pheomelanin, the more abundant the species (Table 2). Eumelanic plumage colour score and body mass

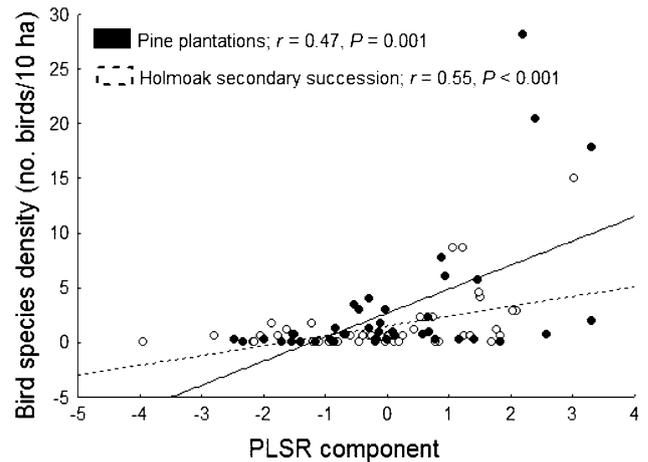


Fig. 1 Relationship between average bird density and the scores of a PLSR component collecting information on ecological, life-history, morphological and phylogenetic traits in 44 bird species detected in 152 census plots in two contrasting restoration trajectories in agricultural landscapes of Central Spain. Phylogenetic effects were computed from the first ten eigenvectors (EV1–EV10) obtained from a principal coordinates analysis applied to the matrix of pairwise phylogenetic distances between the 44 bird species. Regression lines and Pearson correlation tests for both trajectories are shown

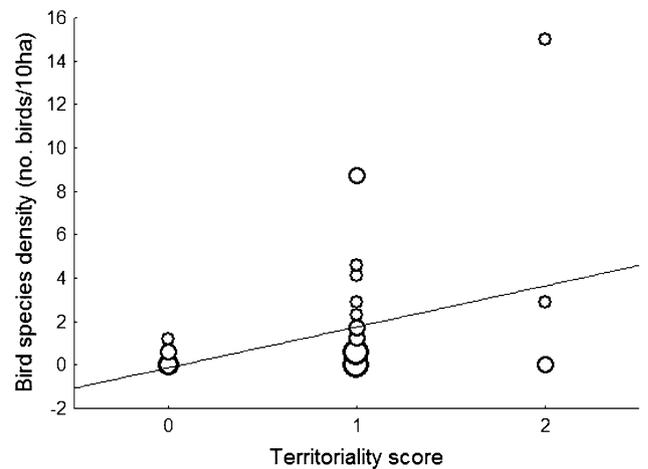


Fig. 2 Relationship between average bird density in secondary succession (woodland) plots and territoriality score of the species (0: species in which males and females do not share resources and feed away from their breeding territory; 1: species in which males and females share resources on their territory only during the breeding season; 2: species in which males and females share resources on their territory all year round). For illustrative purposes, data points increase logarithmically in size with the number of species. The line is the regression line

also contributed, though to a lesser degree (4.4% of the variance), to the information contents of the positive and negative parts, respectively, of the PLSR component (Table 2). EV1–EV10 alone retained 22.9% of the information content of the PLSR component, and as this component accounted for 22.1% of the original variance

(Table 2), the phylogenetic signal in bird density in the plots under passive restoration was $22.1 \times 0.229 = 5.1\%$.

AIC corroborated the conclusions of the PLSR model. After considering the most important factors that contribute to the information content of the PLSR axis (i.e. maximum regional density, plumage dichromatism, pheomelanic plumage score, territoriality, EV1 and EV2), we found that the model that incorporated maximum regional density, plumage dichromatism and pheomelanic plumage score presented the lowest AICc value and the highest weight. There were no other probable models, as the lowest ΔAICc was 4.4 and the lowest quotient between AIC weights was 9.2. Maximum regional density, plumage dichromatism and pheomelanic plumage score were the factors that retained >10% in the information content of the PLSR axis (Table 2).

Bird density in pine plantations

The PLSR model generated an axis that explained 30.0% of the bird density variation in pine plantations. Bird density was significantly correlated with this axis (Fig. 1). This PLSR component was positively related to maximum regional density and to the migratory strategy (i.e. resident species were more abundant than migratory species), and negatively related to body and egg mass (Table 2). Regional habitat breadth was also positively related, though to a lesser degree (4.8%), to this PLSR component (Table 2). EV1–EV10 alone retained 36.6% of the information content of the PLSR component, meaning that the phylogenetic signal in bird density in pine plantations was 11.0%.

The results from AIC also highlighted the importance of the factors that retained >10% of the information content of the PLSR axis; that is, maximum regional density and egg mass (Table 2). Thus, the lowest AICc value corresponded to the model that incorporated maximum regional density, egg mass and EV7, which had a similar probability ($\Delta\text{AICc} = 1.5$) to the model that only included maximum regional density. The quotient of AIC weights for these models was, however, >2 (2.1), suggesting that the model that included maximum regional density, egg mass and EV7 was more likely. The other model comparisons yielded a lowest ΔAICc value of 2.4 and a lowest quotient of AIC weights of 3.4.

Discussion

Overall, we found that densities of bird species occurring at two contrasting trajectories of vegetation restoration in agricultural Mediterranean landscapes, namely natural woodland under secondary succession and pine plantations,

are explained by a range of ecological and life-history traits, melanin-based plumage colouration, and phylogenetic variables. As expected, local bird density increased with the maximum density that the species attain at a regional level and, to a lesser degree, with regional habitat breadth in plots at both trajectories (Tables 1, 2). This finding is in agreement with well-described patterns that follow Brown's (1984) superorganism theory; in other words, those species that better exploit resources will attain higher density, broader habitat breadth and larger geographical ranges (see Rey Benayas et al. 1999 for a review of concepts). However, other species characteristics differed between the two contrasting trajectories of vegetation restoration.

Life-history traits

We recorded the highest observed densities of birds in pine plantations in nonmigratory species with small body masses and low egg masses, while these traits did not help to explain bird density in plots under secondary succession. The effect of territoriality on bird density in pine plantations was small but was in the predicted direction; in other words, bird density tended to be higher in nonterritorial species. These characteristics of bird species in pine plantations are similar to those of successful invasive species (Veltman et al. 1996; Green 1997; Sol and Lefebvre 2000; Blackburn and Duncan 2001; Cassey 2001; Duncan et al. 2001; Sol et al. 2002, 2005).

Not all characteristics of the most abundant species in pine plantations were similar to those of successful invasive species (Table 1). Different studies have shown that the species which achieve a high invasion success are those with large clutch sizes (Duncan et al. 2003) and high behavioural flexibility, as reflected by a large relative brain mass (Sol and Lefebvre 2000; Sol et al. 2002, 2005), while others have shown that sexual plumage dichromatism may also play a role (Sorci et al. 1998; McLain et al. 1999). Neither clutch size, relative brain mass nor plumage dichromatism were significant factors that influenced bird density in the studied pine plantations. However, the characteristics of the most abundant bird species that we recorded in pine plantations may not completely resemble those of spontaneous invading species, because pine plantations do not represent completely novel environments for birds, as this habitat type is actually surrounded by a matrix of croplands and natural woodland. However, the number of species traits shared with good invaders is significantly high for a number of species detected in our census plots, suggesting that the characteristics of invading species can predict establishment success in novel environments generated by pine plantations, even at the small scale considered here.

Bird density in woodland plots was explained by different life-history traits than those that explained bird density in pine plantations. In woodlands, territoriality was the most relevant factor that affected bird density, and this effect was in the opposite direction to that observed in pine plantations (i.e. bird density increased and decreased with intensity of territorial defence in woodlands and pine plantations, respectively, though the effect was weak in the latter). Other studies found that novel environments favour nonterritorial species, whereas more natural sites promote territorial behaviour (Blair and Johnson 2008), probably because absence of territoriality is associated with high population growth, which favours the establishment of populations in novel environments (Duncan et al. 2003). Bird density was higher for dichromatic species than for monochromatic species in woodlands, in contrast to the observed pattern with successful invaders (Sorci et al. 1998; McLain et al. 1999). This suggests that natural selection on plumage conspicuousness may be relaxed in natural environments as compared to novel environments (Møller and Nielsen 2006), as species may not be forced to present behavioural adaptations that are constrained by plumage conspicuousness (Sorci et al. 1998), and may thus suffer lower predation rates in secondary woodlands as compared to pine plantations. We found that bird density was not only unconstrained but was even positively related to plumage dichromatism in woodlands. This is probably due to the fact that plumage dichromatism is associated with intense sexual selection, and polygynous mating prevents the extinction of small populations (Legendre et al. 1999) such as those present in the fragmented natural Mediterranean forests in our study region (Tellería and Santos 1995).

Melanin-based plumage colouration

Our predictions for melanin-based plumage colouration were fulfilled in woodlands instead of pine plantations. As the production of pheomelanin occurs with high levels of endogenous antioxidants (Galván and Alonso-Alvarez 2009; Galván and Solano 2009), maintaining these physiological conditions should be more difficult in novel stressful environments such as pine plantations for species in which natural selection has favoured the genetic mechanism that tips melanogenesis towards the production of pheomelanin (Galván and Solano 2009). The particular antioxidant that must be present at high levels for pheomelanin synthesis (i.e. glutathione, GSH) is under genetic control and is also highly sensitive to several environmental factors in birds and other vertebrates (Sewalk et al. 2001; Galván and Alonso-Alvarez 2009), so stress induced by novel habitat changes can potentially affect GSH levels and exert selection pressures on individuals of species that

differ in their proportions of melanin-based plumage colouration. Indeed, human-induced degradation of forest patches increases corticosterone (a physiological stress-related hormone) levels in birds (Suorsa et al. 2003), and corticosterone increases can produce oxidative stress (e.g. Lin et al. 2004).

Our results suggest that the density of bird species with extensive pheomelanin plumage colouration is limited in woodlands but not in pine plantations. A similar but less strong tendency (Table 2) that occurs in the opposite direction, as expected from the low antioxidant levels required for eumelanogenesis (Galván and Alonso-Alvarez 2008, 2009; Galván and Solano 2009), was found for the proportion of eumelanin plumage. Thus, it is possible that pine plantations induce lower levels of physiological stress in birds than woodlands, even though the pine plantations represent a novel habitat change. This would agree with the observation that, in our study area, bird species richness is higher in pine plantations than in woodland patches (Rey Benayas et al. 2010). It is unlikely that our results are due to pine plantations providing better camouflage benefits to pheomelanin birds than secondary woodlands, as pine plantations support greater development of the tree canopy as compared to secondary woodlands (Díaz et al. 1998; Rey Benayas et al. 2010), while most pheomelanin species probably predominate in more open habitats. Furthermore, we performed our analyses while controlling for the habitat breadth of birds.

Our results highlight the capacity of melanin-based colouration to predict bird density, although this should be tested by performing future studies in which antioxidants are measured in birds in different vegetation restoration trajectories. In bird species that exhibit discrete colour morphs which differ in the type of plumage melanin present, fitness disadvantages have been shown for individuals that belong to the pheomelanin morph as compared to individuals of the eumelanin morph (Brommer et al. 2005), especially in stressful environments (Roulin et al. 2008). These findings may support our prediction that pheomelanin should limit the capacity of individuals to cope with stressful environmental conditions. To our knowledge, this is the first time that melanin-based colouration has been found to be a predictor of population dynamic characteristics at an interspecific level.

Phylogenetic effects on bird density

Finally, we found that bird density presented a low phylogenetic signal in both vegetation restoration trajectories, but that it was twice as large in pine plantations as in woodlands. This suggests that pine plantations limit accessibility for some clades. This limitation is not great, but it is certainly greater than in woodlands, and suggests

the existence of selection pressures on birds establishing in these afforested habitat patches, in addition to those related to life-history traits that reflect the capacity to colonise new environmental conditions.

Conclusions

Our results support from an evolutionary perspective the inability of pine plantations established as a result of cropland reforestation with coniferous species to maintain or increase bird diversity in Mediterranean areas, as reported by other authors (Díaz et al. 1998; Maestre and Cortina 2004). Thus, programs of cropland reforestation in Mediterranean regions should consider a range of tree species and approaches that jointly allow vegetation restoration and biota conservation.

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