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Galván, I. & Benayas, J.M.R. 2011, "Bird species in Mediterranean pine plantations exhibit different characteristics to those in natural reforested woodlands", *Oecologia*, vol. 166, no. 2, pp. 305-316.

Available at <http://dx.doi.org/10.1007/s00442-010-1849-0>

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1 **Pine plantations in Mediterranean abandoned**  
2 **croplands favour bird species that exhibit different**  
3 **characteristics to those in natural reforested**  
4 **woodlands**

5 Short title: Bird species characteristics and restoration

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18 **Abstract** Passive woodland regeneration following cropland abandonment and pine plantations  
19 are two major approaches for vegetation restoration in agricultural landscapes in the  
20 Mediterranean Basin. We compared the effects of these two contrasting approaches on local  
21 bird density in central Spain on the basis of species characteristics, including regional density,  
22 habitat breadth, life-history traits and plumage colouration. Local bird density increased with  
23 regional density and habitat breadth in both woodland and pine plantation plots following  
24 macroecological patterns of bird abundance and distribution. In woodlands, dichromatic species  
25 were more abundant than monochromatic species and bird density increased with the intensity  
26 of territory defense and as the proportion of plumage colour generated by pheomelanin  
27 decreased. Contrary to our prediction, this latter observation suggests that woodlands may  
28 induce higher levels of physiological stress in birds than pine plantations albeit these represent  
29 a novel habitat change. In pine plantations, sedentary species were more abundant than  
30 migratory species and bird density was negatively related to body and egg mass. These traits of  
31 bird species in pine plantations are characteristic of good invading species. The variation in bird  
32 density explained by phylogeny was twice in pine plantations than in woodlands, suggesting  
33 that pine plantations limit accessibility to some clades. Our results support, from an evolutionary  
34 perspective, the described inability of pine plantations on cropland to maintain or increase bird  
35 diversity in Mediterranean agricultural landscapes.

36 **Key-words** Habitat restoration · Life-history · Pheomelanin · Plumage colouration · Vegetation  
37 restoration

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## 43 **Introduction**

44 In the last decades, large tracts of cropland in the world have been abandoned or reforested,  
45 resulting in noticeable effects on biological communities (Laiolo et al. 2004; Rey-Benayas et al.  
46 2007). Cropland abandonment can lead to secondary succession (Rey-Benayas et al. 2008),  
47 which may take several decades in low productivity environments such as Mediterranean areas  
48 (Bonet and Pausas 2004). Cropland reforestation has been proposed to gain forest land at a  
49 shorter timescale than that at which secondary succession occurs naturally. In the case of the  
50 Agrarian Common Policy scheme of the European Union, this has been done through tree  
51 plantations focused on pine species (Meijl et al. 2006). Reforestation with pines creates a  
52 vegetation structure that is different from that present in natural Mediterranean woodlands.  
53 Thus, natural Mediterranean woodlands present higher tree cover and less complexity of  
54 vegetation strata than pine plantations (Sirami et al. 2007; Rey-Benayas et al. 2010), hence the  
55 impacts of these plantations on biodiversity (Donald 2004). Therefore, pine plantations in  
56 croplands represent novel environments to be colonised by native wildlife.

57 Birds represent the group of vertebrates on which the effects of vegetation change in  
58 Mediterranean areas has been most intensively studied (Díaz et al. 1998; Brotons and  
59 Herrando 2001; Santos et al. 2002; Suárez-Seoane et al. 2002; Tellería et al. 2003; Sirami et al.  
60 2007, 2008a,b). These studies have focused on community-level effects. However, the  
61 autoecological characteristics of bird species that colonize newly forested habitats have  
62 received less attention, although the capacity of species to respond to changing landscapes has  
63 been recognized as an ultimate factor driving community dynamics (Sirami et al. 2008a).  
64 Habitat requirements are the autoecological features most often used to explain the success of  
65 bird species in colonising reforested systems in Mediterranean areas, as increases in tree  
66 canopy cover favour woodland species and trigger shrubland species that are characteristic of  
67 Mediterranean native habitats (Díaz et al. 1998; Suárez-Seoane et al. 2002; Sirami et al.  
68 2008a,b). If pine plantations in croplands represent novel environments for native  
69 Mediterranean birds, the autoecological characteristics of species that inhabit them should be  
70 similar to those of successfully colonising or invading species. Additionally, these characteristics

71 may explain the success of birds in pine plantations. To our knowledge, a possible similarity  
72 between species colonising afforested habitats and invasive species has never been tested.

73 Different traits predict the colonization success of birds, the most important of them  
74 being migratory strategy (Veltman et al. 1996; Sol and Lefebvre 2000; Sol et al. 2005), body  
75 mass (Veltman et al. 1996; Green 1997; Sol and Lefebvre 2000; Blackburn and Duncan 2001;  
76 Sol et al. 2002; Cassey et al. 2001), relative brain mass (Sol and Lefebvre 2000; Sol et al. 2002,  
77 2005), clutch size (Veltman et al. 1996; Green 1997; Cassey 2001; Duncan et al. 2001) and  
78 sexual plumage dichromatism (Sorci et al. 1998; McLain et al. 1999). The size of the natural  
79 range of the species also has a role in the case of spontaneous (i.e. not facilitated by human  
80 interventions) invasions (Croci et al. 2007, Møller 2009). Therefore, bird species colonising pine  
81 plantations in Mediterranean areas should present the characteristics of overall invasive species  
82 (see specific predictions below). Here we test this hypothesis by comparing species  
83 characteristics that predict the abundance of birds in two scenarios that represent contrasting  
84 approaches for vegetation restoration in abandoned cropland in Mediterranean landscapes,  
85 namely secondary succession and active vegetation restoration. With this aim we surveyed bird  
86 species in stands under secondary succession (referred to as woodlands hereafter) or planted  
87 with coniferous trees (referred to as pine plantations hereafter) in central Spain, where these  
88 two contrasting trajectories of vegetation restoration depart from recently (< 60 years, mostly  
89 <15 years) abandoned cropland.

90 We made the following predictions (Table 1). (1) Species that are sedentary, have  
91 small body mass and large clutch size should be more abundant than species with opposite  
92 characteristics in pine plantations, as these are characteristics of species with high rates of  
93 population growth and consequently are expected to have higher establishment success in  
94 novel environments (Duncan et al. 2003). Although species with high population growth also  
95 tend to have more variable population sizes, and this could increase their risk of extinction in  
96 novel environments (Duncan et al. 2003; Schaffner 2005), small body size is a predictor of  
97 establishment success across species (Cassey et al. 2001). As egg mass covaries with body  
98 mass across species (Sæther 1987; Poiani and Jeremiin 1994), the same was predicted for egg  
99 mass. (2) Large relative brain mass should be a predictor of species density in pine plantations,

100 as this trait reflects behavioural flexibility (Sol and Lefebvre 2000) and, more specifically, the  
101 diversity of food type and technical innovations of species (Overington et al. 2009). (3) Sexually  
102 monochromatic species should be more abundant than dichromatic species in pine plantations,  
103 as the conspicuous colourations displayed by the latter reduce their capacity to adapt to novel  
104 environments due to predation vulnerability and an increased risk of extinction (Sorci et al.  
105 1998; Møller and Nielsen 2006). (4) Bird species that do not defend territories during the  
106 breeding season should be more abundant in pine plantations than territorial species, as  
107 absence of territoriality is related to high population growth in animals and particularly in birds  
108 (López-Sepulcre and Kokko 2005). Similarly, absence of territoriality has been found to be  
109 related to high invasion success by birds in novel environments produced by urbanization (Blair  
110 and Johnson 2008). By contrast, territorial species should be more abundant in woodlands  
111 (Blair and Johnson 2008). We tested all these predictions controlling for the effect of maximum  
112 observed density at a regional scale, as this variable should be positively related to the density  
113 of species in both contrasting vegetation restoration trajectories. Similarly, we controlled for the  
114 effect of regional habitat breadth (Croci et al. 2007), as high habitat breadth is indicative of  
115 common species that tolerate a wide range of ecological conditions (Carrascal and Seoane  
116 2008).

117 In addition, we tested if bird species density in the two contrasting vegetation restoration  
118 trajectories is differentially predicted by the extension of melanin-based plumage colouration.  
119 The expression of plumage colour generated by melanins is intrinsically related to oxidative  
120 stress (i.e. the imbalance between the production of reactive oxygen species and the state of  
121 the antioxidant and repair machinery; Galván and Alonso-Alvarez 2008, 2009; Galván and  
122 Solano 2009), and novel habitat changes such as pine plantations can cause physiological  
123 stress (i.e. physiological, hormonal or behavioural changes that occur as a response to  
124 unpredictable and noxious stimuli; sensu Romero 2004) in birds (Badyaev 2005), which in turn  
125 can induce oxidative stress (e.g. Lin et al. 2004). Thus, melanization levels of birds may predict  
126 their abundance in the contrasting trajectories of vegetation restoration. The extension of  
127 plumage colour generated by eumelanin (i.e. the darkest form of melanin) may predict species  
128 density in pine plantations because the production of this pigment proceeds under high levels of

129 endogenous oxidative stress, which would increase the tolerance to stress of these species  
130 (Galván and Alonso-Alvarez 2009; Galván and Solano 2009). By contrast, the production of  
131 pheomelanin (i.e. the lightest form of melanin) requires higher levels of antioxidants to proceed  
132 (Galván and Alonso-Alvarez 2009; Galván and Solano 2009), so species with a high proportion  
133 of pheomelanin-based plumage colour may be more limited to establish in pine plantations  
134 (Table 1; see also Møller et al. 2010 for similar predictions for access to dietary antioxidants).  
135 The results of this investigation will provide useful insights for explaining what kind of species is  
136 attracted by active restoration plots from the available species pool (Haila and Järvinen 1983),  
137 as well as mechanistic patterns of colonization of novel habitats by birds that are expanding in  
138 many regions across the world.

139

## 140 **Materials and methods**

### 141 **Study area**

142 We surveyed bird communities in a ca. 6,000 km<sup>2</sup> area of the Mesomediterranean bioclimatic  
143 domain (Rivas-Martínez 1981) located in central Spain. Extreme coordinates for the area are  
144 41°00' N (North), 39°54' N (South), 3°46' W (West) and 2°51' E (East). Altitude ranges between  
145 631 and 1,008 m a.s.l. Climate in this region is continental Mediterranean, with cold winters and  
146 warm dry summers.

147 Natural vegetation chiefly consists of evergreen forests dominated by holm oak *Quercus*  
148 *rotundifolia*. The degradation of these forests has led to more open woodland dominated by *Q.*  
149 *ilex*, *Q. coccifera* or *Juniperus oxycedrus*, or to shrubland dominated by *Cistus ladanifer*,  
150 *Retama sphaerocarpa*, camephytes such as *Thymus* and *Lavandula* species, and herbs (e.g.  
151 *Stipa* spp.). Large tracts of land were reforested with pine species (*Pinus halepensis* and *P.*  
152 *pinea*) after the 1950s and the oldest pine plantations are now considered semi-natural forests  
153 (Peñuelas and Ocaña 1996). Following subsidies from the European Union, some cropland  
154 area was planted almost entirely with *P. halepensis* after 1993. Thus, most afforested

155 abandoned cropland ranges between 3 and 15 years in age at the time we surveyed bird  
156 communities. The natural or semi-natural vegetation and pine plantations intermingle with  
157 farmland mostly consisting of rain-fed cereals and recently abandoned (<4 years old) cropland  
158 under secondary succession.

159

## 160 Bird census

161 We carried out bird censuses during the breeding season (April 28<sup>th</sup> and June 1<sup>st</sup>) of two  
162 consecutive years (2008–2009) by means of single-visit point-counts (Bibby et al. 2000), 10 min  
163 long each, recording all birds heard or seen within a 50-m radius plot. We did not consider  
164 overflying birds. We conducted the censuses by the same two well trained field technicians on  
165 windless and rainless days, between sunrise and 1100 h GMT in the morning. Point counts do  
166 not provide absolute densities, but relative abundances. Nevertheless, the small area covered  
167 by the plots (0.78 ha), and the relatively long time devoted to bird counts, maximizes the  
168 detection probability of species and, thus, the accurate estimations of their abundance (Shiu  
169 and Lee 2003). Bird censuses were conducted in pine plantations and natural woodlands, and  
170 also in recently abandoned crops (< 4 years old) surrounding them because they contain  
171 species that could potentially occupy pine plantations and natural woodlands. We detected a  
172 total of 44 bird species (Online Resource 1). From these, two were present in neither pine  
173 plantations nor natural woodlands and were only detected in croplands (i.e. common skylark  
174 *Alauda arvensis* and common quail *Coturnix coturnix*; see Online Resource 1). These two  
175 species were nevertheless included in the analyses because they can potentially occupy pine  
176 plantations and natural woodlands. The remaining species were present in pine plantations  
177 and/or natural woodlands.

178         Prior to sampling, we first explored the entire territory by means of aerial photographs  
179 and Google Earth, and then visited the potential survey localities to locate the census plots. A  
180 total number of 152 census plots were obtained in 48 localities distributed throughout the study  
181 area in an attempt to sample the whole availability of habitats and the gradient of altitudes (we  
182 censused every plots in one year only to maximize a wide regional coverage). We spanned



183 censuses of the different habitats considered throughout the study period, avoiding censusing  
184 certain habitats in only one year. We did not observe any clear inter-annual variation in bird  
185 abundance of the study species, so we pooled all the censuses obtained in both years. We geo-  
186 referenced the census plots with a portable GPS and interspersed these by at least 200 m from  
187 each other. We located them in order to include homogeneous habitat types of the study area.  
188 These main habitat types were abandoned cropland, pastureland, camephyte shrubland,  
189 shrubland (mainly of the genera *Cistus* and *Genista*), several stages of holm oak succession to  
190 mature stands, and a range of afforested croplands with pines (from seedlings to pine stands  
191 ca. 60 years old). We used these habitat types as a guideline to select the survey localities. Of  
192 the 152 plots, 62 were located in stands under woodland secondary succession, 75 in pine  
193 plantation stands, and 15 in recently (<4 years) abandoned cropland stands. A full description of  
194 habitat features in the census plots can be found in Rey Benayas et al. (2010).

195

## 196 Bird regional density and habitat breadth

197 We summarized regional patterns of distribution-abundance of the bird species detected in the  
198 152 point counts according to maximum density and habitat breadth of species in the  
199 biogeographic region where the study area is included (Central Spain Mesomediterranean  
200 region). We estimated the maximum regional density (birds/km<sup>2</sup>) recorded in 13 major habitat  
201 types of the study region as a measure of the maximum ecological abundance that a species  
202 can attain in its most favourable environment. We established these 13 habitat types  
203 considering vegetation structure, floristic composition and human impact and these account for  
204 more than 95% of the surface of the whole study area. They were the following: two types of  
205 urban environments (according to building height and density), non-irrigated arable crops,  
206 irrigated arable crops, mixed orchards, vineyards, olive plantations, two types of shrubland  
207 (according to shrub height and density), pasturelands, pinewoods, deciduous woodlands and  
208 holm oak woodlands. We obtained the data base for this analysis from the Spanish SACRE  
209 program (monitoring of common breeding birds in Spain), using 3,417 five-min point-counts  
210 censused in 2004-2006, and distributed over the study area. We obtained absolute densities for

211 this data base using detectability provided by Carrascal and Palomino (2008) of the same  
212 census program.

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

$$215 \quad \text{HB} = [(\sum p_i^2)^{-1}]/13$$

216 where  $p_i$  is the proportion of the density for each species measured in the habitat  $i$  (dividing  
217 density in habitat  $i$  by the sum of all maximum densities recorded in the 13 habitat types). This  
218 index ranges between 1 (evenly distributed across the 13 habitat types) and 1/13 (only present  
219 in one habitat type).

220

## 221 Morphological and life-history traits of birds

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

229 We took information on clutch size, egg mass and territorial behaviour from Lislevand et  
230 al. (2007). We defined territorial behaviour by a three-level variable: score 0: species in which  
231 males and females do not share resources and feed away from their breeding territory; score 1:  
232 species in which males and females share resources on their territory only during the breeding  
233 season; score 2: species in which males and females share resources on their territory all year  
234 round (Lislevand et al. 2007). These scores were consistent among observers ( $r_s = 0.628 -$   
235  $0.674$ ,  $n = 1454 - 1629$  species,  $P < 0.001$ ; Lislevand et al. 2007). Territorial behaviour was not  
236 available for five species (Online Resource 1). We took information on the migratory strategy of

237 birds (trans-Saharan migrant, score 0 vs. resident, score 1) in the study area from Seoane and  
238 Carrascal (2007).

239

## 240 Bird plumage colouration

241 We obtained information on sexual dichromatism in plumage by examining illustrations in  
242 Cramp and Simmons (1977-1994) and photographs of birds captured in Spain from the  
243 Identification Atlas of Birds of Aragón (2010). We also examined text descriptions of plumage  
244 characteristics in these sources. We considered that a species was sexually dichromatic (score  
245 1) when both sexes exhibited a conspicuous and clearly distinguishable difference in plumage  
246 colouration. Otherwise the species were categorised as monochromatic (score 0). Seddon et al.  
247 (2010) have recently shown that human visual assessment of sexual dichromatism is positively  
248 correlated with the avian perception of the trait. Although species that we consider sexually  
249 monochromatic may indeed be dichromatic regarding ultraviolet (UV) reflectance, to which we  
250 are blind, UV reflectance is generated by structural feather colourations (Prum 2006). However,  
251 most species in our list do not present such colourations, but they are mainly coloured by  
252 melanins. Thus, it is not likely that a classification of mono-/dichromatic species that consider  
253 UV reflectance significantly changes our conclusions.

254 Eumelanic and pheomelanic traits are generally of distinctive colours, the formers being  
255 responsible for black and grey colours and the latter for yellowish, reddish, chestnut and brown  
256 colours (Toral et al. 2008). Eumelanin and pheomelanin normally occur simultaneously in the  
257 tissues (Ozeki et al. 1997), but the darker colours conferred by eumelanin (Toral et al. 2008)  
258 make evident the lower content of this pigment in chestnut and brown colours as compared to  
259 black and grey colours (Galván and Alonso-Alvarez 2009). Furthermore, many bird species  
260 present feather melanin contents of high purity (> 90% of either eumelanin or pheomelanin;  
261 McGraw and Wakamatsu 2004; J.J. Negro pers. com.). Therefore, we considered that black and  
262 grey plumage colours were predominantly generated by eumelanin, while chestnut and brown  
263 colours were predominantly generated by pheomelanin. We did not consider conspicuous  
264 yellow or red colourations suspicious of being generated by other pigments (i.e. carotenoids),

265 unless chemically identified as melanin-based by Toral et al. (2008). Although a rough  
266 approximation to the real proportion of eumelanic and pheomelanic plumage, the assumption  
267 that black-grey colours are eumelanic and brown-chestnut colours are pheomelanic should be  
268 adequate for comparative purposes (Owens and Hartley 1998). Thus, one of us (IG) quantified  
269 the proportion of melanic plumage parts by examining illustrations in Cramp and Simmons  
270 (1977-1994) and photographs of birds captured in Spain from the Identification Atlas of Birds of  
271 Aragón (2010). Several authors have used this method previously (see, e.g., John 1995;  
272 Yezerinac and Weatherhead 1995; Caro 2009), and it has been shown to be a reliable method  
273 of quantifying different components of plumage colour that is even correlated with the avian  
274 perception of colour (del Val et al. 2009; Seddon *et al.* 2010). We examined illustrations of both  
275 resting and flying birds. We followed the method used by Beauchamp and Heeb (2001) and  
276 Galván (2008) to obtain estimates of the proportion of eu- and pheomelanic colour present in  
277 the plumage of each species, assigning scores that ranged from 0 (total lack of melanic colour)  
278 to 5 (all melanic). When a species was sexually dichromatic regarding the type of melanin-  
279 based colouration (i.e. eumelanic vs. pheomelanic), we averaged eumelanic and pheomelanic  
280 scores obtained for males and females. Our scores were highly correlated with those assigned  
281 by an independent observer (eumelanin-based colour score:  $r_s = 0.85$ ,  $n = 44$  species,  $P <$   
282  $0.0001$ ; pheomelanin-based colour score:  $r_s = 0.93$ ,  $n = 44$  species,  $P < 0.0001$ ).

283

## 284 Data analyses

285 We analysed the relationships between the response variables (average bird density in the two  
286 contrasting vegetation restoration trajectories) and ecological, morphological and life-history  
287 traits of the species (predictor variables) by means of Partial Least Squares Regressions  
288 (hereafter PLSR; Carrascal et al. 2009), using the species as the sample unit ( $n = 44$ ). This  
289 statistical tool is an extension of multiple regression analysis where associations are established  
290 with factors extracted from predictor variables that maximize the explained variance in the  
291 dependent variable. These factors are defined as a linear combination of independent variables,  
292 so the original multidimensionality is reduced to a lower number of orthogonal factors to detect

293 structure in the relationships between predictor variables and between these factors and the  
294 response variable. The extracted factors account for successively lower proportions of original  
295 variance. We calculated the relative contribution of each variable to the derived factors by  
296 means of the square of predictor weights. Results obtained with PLSR are similar to those from  
297 conventional multiple regression techniques; however, it is extremely robust to the effects of  
298 sample size and degree of correlation between predictor variables, which makes PLSR  
299 especially useful when sample size is low and in cases of severe multicollinearity (Carrascal et  
300 al. 2009). We introduced all predictor variables as continuous variables (log-transformed) in the  
301 PLSR models, except migratory strategy and sexual dichromatism that were introduced as  
302 categorical factors.

303 Bird species are evolutionarily related through phylogeny, and therefore, they should not  
304 be treated as independent sample units (Felsenstein 1985). Therefore, the effect of common  
305 ancestry among taxa can lead to an overestimation of degrees of freedom if phylogenetic  
306 relationships are not taken into account. We used phylogenetic eigenvector regression (PVR) to  
307 quantify the amount of phylogenetic signal and to correct for it in the analysis of the relationship  
308 between bird density and ecological, morphological and life-history traits (Diniz-Filho et al.  
309 1998). Diniz-Filho and Torres (2002) and Martins et al. (2002) tested several comparative  
310 methods (Felsenstein's independent contrasts, autoregressive method, PVR, and phylogenetic  
311 generalized least squares) and found that PVR yields good statistical performance regardless of  
312 the details of the evolutionary mode used to generate the data and provides similar results to  
313 other methods, with very good (i.e., low) error types I and II. Moreover, PVR does not assume  
314 any *a priori* evolutionary model (an advantage if the true evolutionary model is unknown or if it is  
315 too complex) and has similar statistical performance even under evolutionary processes distinct  
316 from Brownian motion.

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

321 We first performed a Principal Coordinates Analysis (PCORD) on the matrix of pairwise  
322 phylogenetic distances between the 44 bird species (after a double-center transformation). In a  
323 second step we selected the first 10 eigenvectors to account parsimoniously for the  
324 phylogenetic signal. Eigenvectors extracted from double-centered phylogenetic distance  
325 matrices are able to detect the main topological features of the cladogram under different  
326 sample sizes or number of taxa used in the analyses (Diniz-Filho et al. 1998). We found that the  
327 original matrix of phylogenetic distances between the 44 bird species and the reproduced matrix  
328 of distances estimated based on the first 10 eigenvectors were very similar (Mantel test with  
329 999 randomised matrices to estimate significance:  $r = 0.920$ ,  $P < 0.001$ ; test carried out using  
330 PopTools 3.1; Hood 2009). We used these eigenvectors as additional predictor variables in the  
331 PLSR models described above in order to control for phylogeny.

332 We used the Akaike information criterion (AIC) (Burnham and Anderson 2004) to  
333 corroborate the results obtained with the PLSR models. With this aim we selected the most  
334 important predictor variables that resulted from the PLSR models (i.e. those with predictor  
335 weights that retained  $> 5\%$  of the information content of the PLSR axes) and performed a  
336 Generalized Linear Model (GLM) for the dependent variables and these predictor variables. We  
337 calculated the Akaike's second order information criterion (AICc) and weights ( $w$ ) for all possible  
338 models with these variables, considering that two models were equally probable if the difference  
339 in AICc ( $\Delta AICc$ ) or the division of their weights was  $> 2$  (Burnham and Anderson 2004). We  
340 carried out all analyses using MVSP version 3.13 (Covach Computing Services) and Statistica  
341 8.0 (StatSoft Inc.).

342

## 343 **Results**

### 344 **Bird density in woodlands**

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

348 dichromatic species were more abundant than monochromatic species), and territorial  
349 behaviour (i.e. bird density increased with the intensity of territory defense) (Table 2; Fig. 2). By  
350 contrast, the PLSR component was negatively related to pheomelanic plumage colour score,  
351 indicating that the lower the proportion of plumage generated by pheomelanin, the more  
352 abundant the species (Table 2). Eumelanic plumage colour score and body mass also  
353 contributed, though to a lesser degree (4.4% of variance), to the information content of the  
354 positive and negative parts, respectively, of the PLSR component (Table 2). EV1-EV10 alone  
355 retained 22.9% of the information content of the PLSR component, and as this component  
356 accounted for 22.1% in original variance (Table 2), the phylogenetic signal in bird density in  
357 plots under passive restoration was  $22.1 \times 0.229 = 5.1\%$ .

358 AIC corroborated the conclusions of the PLSR model. After considering the most  
359 important factors contributing to the information content of the PLSR axis (i.e. maximum  
360 regional density, plumage dichromatism, pheomelanic plumage score, territoriality, EV1 and  
361 EV2), we found that the model entering maximum regional density, plumage dichromatism and  
362 pheomelanic plumage score presented the lowest AICc value and the highest weight. There  
363 were no other probable models, as the lowest  $\Delta AICc$  was 4.4 and the lowest division between  
364 AIC weights was 9.2. Maximum regional density, plumage dichromatism and pheomelanic  
365 plumage score were the factors that retained  $> 10\%$  in the information content of the PLSR axis  
366 (Table 2).

367

### 368 Bird density in pine plantations

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

375 the information content of the PLSR component, meaning that the phylogenetic signal in bird  
376 density in pine plantations was 11.0%.

377 The results from AIC also highlighted the importance of the factors that retained > 10%  
378 in the information content of the PLSR axis, that is, maximum regional density and egg mass  
379 (Table 2). Thus, the lowest AICc value corresponded to the model entering maximum regional  
380 density, egg mass and EV7, which was of similar probability ( $\Delta AICc = 1.5$ ) than the model that  
381 only included maximum regional density. The division of AIC weights for these models was,  
382 however, > 2 (2.1), suggesting that the model entering maximum regional density, egg mass  
383 and EV7 was more likely. The rest of model comparisons yielded a lowest value for  $\Delta AICc$  of  
384 2.4 and for AIC weights division of 3.4.

385

## 386 **Discussion**

387 Overall, we found that density of bird species occurring at two contrasting trajectories of  
388 vegetation restoration in agricultural Mediterranean landscapes, namely natural woodland under  
389 secondary succession and pine plantations, are explained by a range of ecological and life-  
390 history traits, melanin-based plumage colouration, and phylogenetic variables. As expected,  
391 local bird density increased with maximum density that the species attain at a regional level  
392 and, to a lesser degree, with regional habitat breadth in plots at both trajectories (Tables 1 and  
393 2). This finding is in agreement with well described patterns that follow Brown's (1984)  
394 superorganism theory, i.e those species that better exploit resources will attain higher density,  
395 broader habitat breadth and larger geographical ranges (see Rey-Benayas et al. 1999 for a  
396 review of concepts). However, other species characteristics differed between the two  
397 contrasting trajectories of vegetation restoration.

398

399 **Life-history traits**



400 We recorded the highest observed densities of birds in pine plantations in species with small  
401 body mass, low egg mass and do not migrate, while these traits did not contribute to explain  
402 bird density in plots under secondary succession. The effect of territoriality on bird density in  
403 pine plantations was low but in the predicted direction, i.e. bird density tended to be higher in  
404 non-territorial species. These characteristics of bird species in pine plantations are similar to  
405 those of good invasive species (Veltman et al. 1996; Green 1997; Sol and Lefebvre 2000;  
406 Blackburn and Duncan 2001; Cassey 2001; Duncan et al. 2001; Sol et al. 2002, 2005).

407 Not all characteristics of the most abundant species in pine plantations were similar to  
408 those of good invasive species (Table 1). Different studies have shown that species  
409 accomplishing high invasion success are those with large clutch size (Duncan et al. 2003) and  
410 have high behavioural flexibility as reflected by large relative brain mass (Sol and Lefebvre  
411 2000; Sol et al. 2002, 2005), and others show that sexual plumage dichromatism may also play  
412 a role (Sorci et al. 1998; McLain et al. 1999). Neither clutch size, relative brain mass nor  
413 plumage dichromatism importantly contributed to explain bird density in the studied pine  
414 plantations. However, the characteristics of the most abundant bird species that we recorded in  
415 pine plantations may not completely resemble those of spontaneous invading species because  
416 pine plantations do not represent completely novel environments for birds as this habitat type is  
417 actually surrounded by a matrix of croplands and natural woodland. However, the number of  
418 species traits shared with good invaders is significantly high for the number of species detected  
419 in our census plots, suggesting that the characteristics of invading species can predict  
420 establishment success in novel environments generated by pine plantations even at a small  
421 scale as that considered here.

422 Bird density in woodland plots was explained by different life-history traits than those  
423 that explained bird density in pine plantations. In woodlands, territoriality was the most relevant  
424 factor that affected bird density, and this effect was in the opposite direction to that observed in  
425 pine plantations (i.e. bird density increased and decreased with the intensity of territory defense  
426 in woodlands and pine plantations, respectively, though in the latter the effect was weak). Other  
427 studies found that novel environments favour non-territorial species, whereas more natural sites  
428 promote territorial behaviour (Blair and Johnson 2008), probably because the absence of

429 territoriality is associated with high population growth that favours the establishment of  
430 populations in novel environments (Duncan et al. 2003). Bird density in woodlands was higher  
431 in dichromatic species than in monochromatic species, in contrast to the observed pattern in  
432 good invading species (Sorci et al. 1998; McLain et al. 1999). This suggests that natural  
433 selection on plumage conspicuousness may be relaxed in natural environments as compared to  
434 novel environments (Møller and Nielsen 2006), as species may not be forced to present  
435 behavioural adaptations that are constrained by plumage conspicuousness (Sorci et al. 1998),  
436 and may thus suffer lower predation rates in secondary woodlands as compared to pine  
437 plantations. We found that bird density was not only unconstrained, but even positively related  
438 to plumage dichromatism in woodlands. This is probably due to the fact that plumage  
439 dichromatism is associated with intense sexual selection, and polygynous mating prevents  
440 extinction of small populations (Legendre et al. 1999) such as those present in fragmented  
441 natural Mediterranean forests in our study region (Tellería and Santos 1995).

442

#### 443 Melanin-based plumage colouration

444 Our predictions for melanin-based plumage colouration were fulfilled in woodlands instead of  
445 pine plantations. As the production of pheomelanin occurs with high levels of endogenous  
446 antioxidants (Galván and Alonso-Alvarez 2009; Galván and Solano 2009), maintaining these  
447 physiological conditions should be constrained in novel stressful environments such as pine  
448 plantations for species in which natural selection has favoured the genetic mechanism that tips  
449 melanogenesis towards the production of pheomelanin (Galván and Solano 2009). The  
450 particular antioxidant whose levels must be high for pheomelanin synthesis (i.e. glutathione,  
451 GSH), is not only under genetic control, but also highly sensitive to several environmental  
452 factors in birds and other vertebrates (Sewalk et al. 2001; Galván and Alonso-Alvarez 2009), so  
453 stress induced by novel habitat changes can potentially affect GSH levels and exert selection  
454 pressures on individuals of species that differ in the proportion of melanin-based plumage  
455 colouration. Indeed, human-induced degradation of forest patches increases corticosterone (i.e.

456 a physiological stress-related hormone) levels in birds (Suorsa et al. 2003), and corticosterone  
457 increases can produce oxidative stress (e.g. Lin et al. 2004).

458         Our results suggest that the density of bird species with large extension of pheomelanin  
459 plumage colouration is limited in woodlands but not in pine plantations. A similar tendency of  
460 lower magnitude (Table 2) but in the opposite direction, as expected from the low antioxidant  
461 levels required for eumelanogenesis (Galván and Alonso-Alvarez 2008, 2009; Galván and  
462 Solano 2009), was found for the proportion of eumelanin plumage. Thus, it is possible that pine  
463 plantations, albeit representing a novel habitat change, induce lower levels of physiological  
464 stress in birds than woodlands. This would agree with the observation that, in our study area,  
465 bird species richness is higher in pine plantations than in woodland patches (Rey-Benayas et al.  
466 2010). It is not likely that our results are due to pine plantations providing better camouflage  
467 benefits to pheomelanin birds than secondary woodlands, as pine plantations support a larger  
468 development of tree canopy as compared to secondary woodlands (Díaz et al. 1998; Rey-  
469 Benayas et al. 2010), while most pheomelanin species probably predominate in more open  
470 habitats (pers. obs.). Furthermore, we made our analyses controlling for the habitat breadth of  
471 birds.

472         Our results highlight the capacity of melanin-based colouration to predict bird density,  
473 although they should be tested by future studies measuring antioxidants in birds in the different  
474 vegetation restoration trajectories. In bird species that exhibit discrete colour morphs differing in  
475 the type of plumage melanin, fitness disadvantages have been shown for individuals belonging  
476 to the pheomelanin morph as compared to individuals of the eumelanin morph (Brommer et al.  
477 2005), especially in stressful environments (Roulin et al. 2008). These findings may support our  
478 prediction that pheomelanin should limit the capacity of individuals to cope with stressful  
479 environmental conditions. To our knowledge, this is the first time that melanin-based colouration  
480 is found to be a predictor of population dynamic characteristics at an interspecific level.

481

482 Phylogenetic effects on bird density

483 Finally, we found that bird density presented a low phylogenetic signal in both vegetation  
484 restoration trajectories, and that it was twice as large in pine plantations as in woodlands. This  
485 suggests that pine plantations limit accessibility for some clades. This limitation is not high, but  
486 certainly higher than in woodlands, and suggests the existence of selection pressures acting on  
487 birds establishing in these afforested habitat patches in addition to those related to life-history  
488 traits that reflect the capacity to colonize new environmental conditions.

489

## 490 Conclusions

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

497

498 **Acknowledgements** We are indebted to Irene Razola and Jorge Meltzer for their assistance to  
499 survey birds and to Luis M. Carrascal for suggestions that greatly improved the manuscript. This  
500 research was funded by the Spanish Ministry of Science and Education (project CGL2007-  
501 60533-BOS) and the Madrid Government REMEDINAL project (S2009AMB-1783).

502

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705 **Table 1** Predictions made for bird species density in two contrasting trajectories of vegetation restoration in agricultural landscapes of Central Spain regarding  
 706 ecological, life-history and morphological traits, and results obtained in the present study considering that the most abundant bird species establishing in a  
 707 novel habitat type (i.e. pine plantations) should exhibit characteristics of good invaders. '+' and '-' indicate that the effect on bird density should be positive and  
 708 negative, respectively. '\*' means that the result was in the predicted direction, but the magnitude of the effect was lower than for other factors as deduced  
 709 from the PLSR models (see Table 2).

Predictor variable	Prediction for passive restoration (secondary succession)	Prediction confirmed	Prediction for active restoration (pine plantations)	Prediction confirmed
<i>Regional population effects</i>				
Maximum regional density	+	Yes	+	Yes
Regional habitat breadth	+	Yes*	+	Yes*
<i>Life-history traits</i>				
Sedentariness	No effect	Yes	+	Yes
Territoriality	+	Yes	-	Yes*
Clutch size	No effect	Yes	+	No
Egg mass	No effect	Yes	-	Yes
<i>Morphology and colouration</i>				

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

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718 **Table 2** Predictor weights of the two Partial Least Squares Regression (PLSR) analyses  
 719 explaining the relationship between the average density of 44 bird species occurring in 152  
 720 surveyed census plots (50 m radius; birds/10 ha) in two contrasting trajectories of vegetation  
 721 restoration in agricultural landscapes of Central Spain (response variables) and ecological, life-  
 722 history and morphological traits of the species (predictor variables). Additional predictor  
 723 variables account for variability due to phylogenetic effects, which are computed from the first  
 724 10 eigenvectors (EV1 to EV10) obtained from Principal Coordinates Analysis applied to the  
 725 matrix of pairwise phylogenetic distances between the 44 bird species. Predictor weights  
 726 represent the contribution of each predictor variable to the PLSR axis. Predictor weights that  
 727 retain > 5% of the information content of the PLSR axis are shown in bold type.

Predictor variable	Passive restoration (secondary succession)	Active restoration (pine plantations)
<i>Regional population effects</i>		
Maximum regional density (no. birds/10 ha)	<b>0.33</b>	<b>0.45</b>
Regional habitat breadth	0.15	0.22
<i>Life-history traits</i>		
Migratory strategy	0.19	<b>0.27</b>
Territoriality	<b>0.40</b>	-0.13
Clutch size	-0.04	-0.14
Egg mass (g)	-0.18	<b>-0.31</b>
<i>Morphology and colouration</i>		
Body mass (g)	-0.21	<b>-0.25</b>
Relative brain mass	0.22	-0.04
Sexual dichromatism	<b>0.24</b>	0.10
Eumelanic plumage colour score	0.21	-0.03
Pheomelanic plumage colour score	<b>-0.34</b>	0.12
<i>Phylogenetic effects</i>		
EV1	<b>-0.24</b>	0.18



EV2	<b>-0.29</b>	-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	<b>0.29</b>
EV8	-0.12	-0.14
EV9	-0.01	<b>0.26</b>
EV10	0.20	<b>0.25</b>
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% variance accounted for	22.1	30.0
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Eigenvalue	2.25	2.02

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742 **Fig. 1.** Relationship between average bird density and the scores of a PLSR component  
743 collecting information on ecological, life-history, morphological and phylogenetic traits in 44 bird  
744 species detected in 152 census plots in two contrasting restoration trajectories in agricultural  
745 landscapes of Central Spain. Phylogenetic effects were computed from the first 10 eigenvectors  
746 (EV1 to EV10) obtained from Principal Coordinates Analysis applied to the matrix of pairwise  
747 phylogenetic distances between the 44 bird species. Regression lines and Pearson correlation  
748 tests for both trajectories are shown.

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

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782 Figure 1

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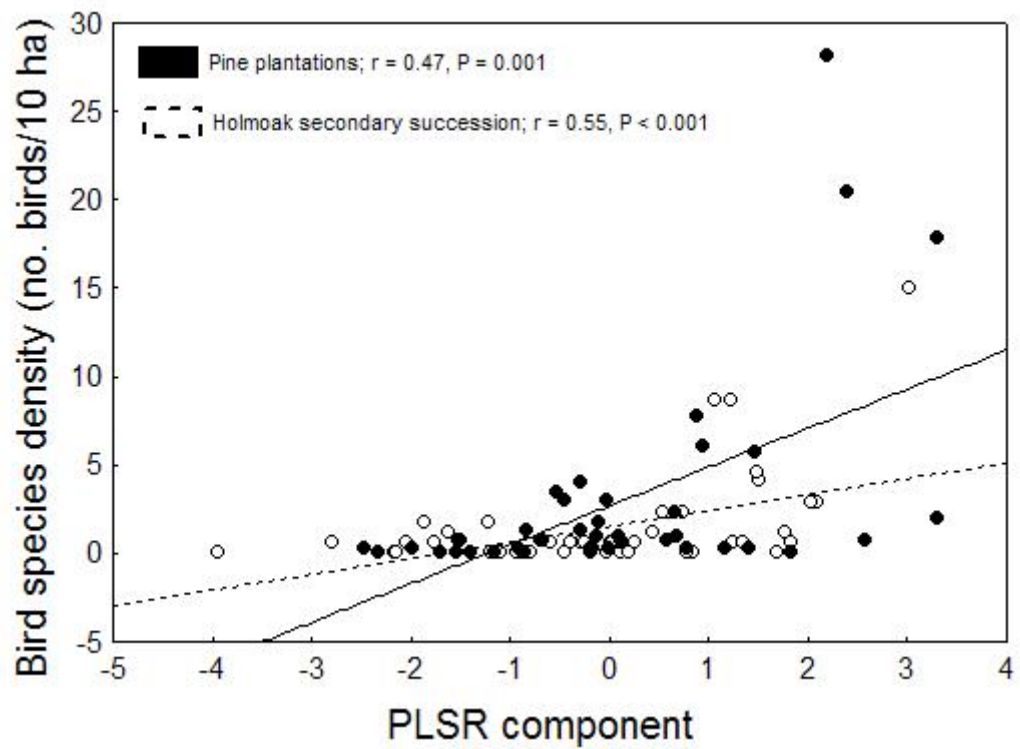
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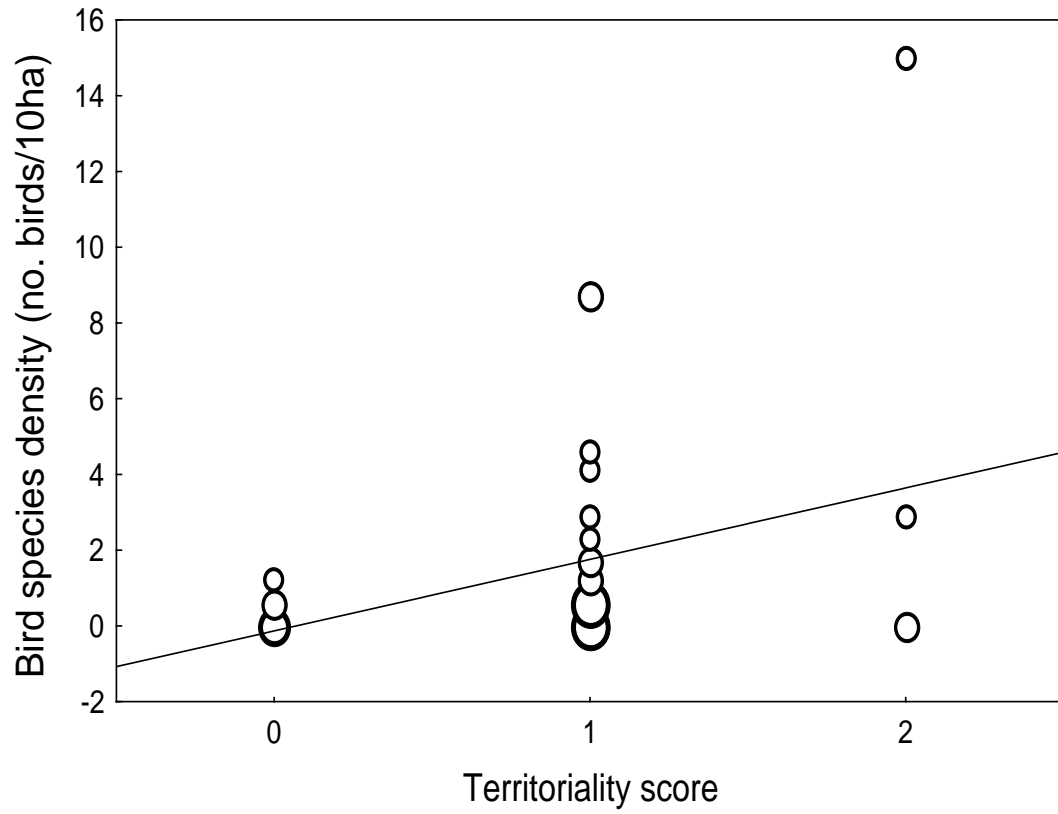


Figure 2