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1 **Differential effects of vegetation restoration in Mediterranean**
2 **abandoned cropland by secondary succession and pine**
3 **plantations on bird assemblages**

4

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15

1 **Abstract**

2 Two contrasting trajectories for vegetation restoration in agricultural landscapes are
3 secondary succession following cropland abandonment that can regenerate woodlands
4 (passive restoration) and conversion of cropland to tree plantations (active restoration),
5 which have mostly focused on pine species in the Mediterranean Basin. We compared
6 the effects of these two contrasting trajectories of vegetation restoration on bird
7 assemblages in central Spain. Vegetation structure differed in the two restoration
8 trajectories, pine plantations attaining higher tree cover and height (31% and 4.1 m,
9 respectively) but lower strata complexity than secondary shrubland and holm oak
10 woodland (which attained 10% and 1.4 m of tree cover and height, respectively). Bird
11 species richness differed in stands under active or passive restoration trajectories, the
12 former collecting a higher total number of species (4.2 species per 0.78 ha plot) than the
13 latter (3.5 species per plot). The number of forest species increased with vegetation
14 maturity in both restoration trajectories, but especially in stands under active restoration.
15 The occurrence of woodland generalist species increased and of species inhabiting open
16 habitats decreased in actively restored stands, being some of these latter species of high
17 conservation priority in the European context but relatively common at the regional
18 level. Bird species inhabiting pine plantations had broader habitat breadth at the
19 regional level than those inhabiting secondary shrublands and woodlands. Maximum
20 regional density did not differ between both restoration trajectories, but it increased with
21 development of the herbaceous layer only at the secondary succession trajectory. The
22 relative importance of species of European biogeographic origin was higher in mature
23 pine plantations (58.9% of total bird abundance) than in mature holm oak woodlands
24 (34.4%), whereas that of Mediterranean species was considerably higher in the latter
25 (40.1%) than in the former (20%). Bird assemblages of relatively small patches of pine

1 plantations are unable to reflect the regional avifauna, in contrast with the relationships
2 between local and regional assemblage characteristics that can be found in isolated
3 natural forests. We conclude that programs of vegetation restoration should base upon a
4 range of approaches that include passive restoration, active restoration with a variety of
5 tree and shrub species, and mixed models to conciliate agricultural production,
6 vegetation restoration and conservation of target species.

7

8 **Key words:** bird composition; conservation; habitat breadth; regional avifauna; species
9 richness; vegetation complexity

10

1 **1. Introduction**

2 The structural complexity of vegetation is a major factor influencing bird communities,
3 including their characteristics of species composition, diversity, and local abundance
4 (Wiens, 1989). Within a particular region or landscape, human activities may
5 profoundly modify land cover and vegetation structure and, consequently, may affect
6 the composition and abundance of bird species (Blondel and Aronson, 1999; Heikkinen
7 et al., 2004). For instance, large tracts of cropland have been abandoned or reforested in
8 the world in recent decades, with noticeable effects on biological communities
9 (Poschlod et al., 2005; Rey Benayas et al., 2007; Gómez-Aparicio et al., 2009).

10 Agricultural intensification and deforestation in order to create farmland can
11 occur alongside extensive farmland abandonment which, in turn, can lead to succession
12 back to the forest (Rey Benayas et al., 2008). Secondary succession is usually rapid in
13 high productivity environments such as the tropics (Muñiz et al., 2006), but slow in low
14 productivity environments such as Mediterranean areas (Bonet and Pausas, 2004).
15 Subsidies from the Agrarian Common Policy scheme of the European Union to land
16 owners have motivated the conversion of cropland to tree plantations. Tree plantations
17 in dry Mediterranean regions have mostly focused on pine species, though other species
18 such as exotic *Eucalyptus* spp. and endemic *Quercus* species have been also widely
19 used (Reino et al., 2009). This practice allows former croplands to present more tree
20 cover than if a secondary succession leading to natural maquis or broad-leaved
21 woodland had occurred during a similar period of time.

22 Habitat changes induced by land abandonment have been demonstrated to
23 determine bird distribution patterns in large areas of the Mediterranean Basin (Preiss et
24 al., 1997; Sirami et al., 2007, 2008; Vallecillo et al., 2008). The Mediterranean region is
25 one of the most altered hotspots by human activities in the world. Recent changes in

1 land use / land-cover patterns usually imply increases in forests (especially in mountain
2 areas), and marked decreases in pasturelands and extensively cultivated areas, that are
3 associated with increases in forest birds (e.g., Falcucci et al., 2007). Landscape changes
4 induced by land abandonment mainly favor the short-term development of shrubland,
5 and may potentially increase the range of potential habitats used by threatened open
6 habitat bird species at the landscape scale. On the other hand, forest bird species could
7 not recognize young woodland habitat patches embedded within unsuitable habitat (e.g.,
8 arable crops) as favorable environments (Virkkala et al., 2004). Thus, the distribution of
9 woodland bird species will be mainly determined by their ability to respond to
10 landscape changes and to colonize new habitats generated by secondary succession or
11 tree plantations.

12 Increasing evidence suggests that tree plantations can support some native
13 biodiversity and may even provide occasional habitat for vulnerable species,
14 contributing to biodiversity conservation (Hartley, 2002; Lindenmayer and Hobbs,
15 2004). Nevertheless, plantations usually support modified assemblages than those found
16 in natural habitats (Donald, 2004), and bird species richness may be reduced when
17 natural forests are replaced by plantations. Moreover, the assemblages in plantations
18 generally hold more species of lower conservation concern than forests; for example,
19 Sirami et al. (2007) found that as most species of high conservation profile in the
20 Mediterranean are tied to open or to heterogeneous transitional habitats, changes in
21 vegetation structure linked to land abandonment and tree plantations raise questions
22 concerning their persistence in the future. Patch size of tree plantations also exert a
23 prominent role in woodland species occurrence. Thus, Díaz et al. (1998) found that
24 fragment size accounted for ca. 70% of the variation in forest bird species of pine
25 plantations in Spanish Mediterranean plateaux, and Brotons and Herrando (2001) found

1 that most of the woodland bird species analyzed in the north-western Mediterranean
2 Basin were influenced by the spatial arrangement of forest fragments, especially size
3 but also by distance to corridors and to large continuous forest habitats. Decreases in the
4 number of species in small woodland fragments may be explained according to the loss
5 of habitat (e.g. random sample hypothesis, Connor and McCoy, 1979) and to the
6 indirect effects of fragmentation related to increased isolation or an increase in edge
7 area (Van Drop and Opdam, 1987; Opdam, 1991).

8 Changes in bird diversity induced by land abandonment or tree plantations are
9 dependent as well on the position of the study region within a biogeographical context
10 and on the biogeographic origin of species. Suárez-Seoane et al. (2002) found, at the
11 boundary of the Mediterranean and Eurosiberian regions in northern Spain, that avian
12 diversity increased with the vegetation successional gradient for Eurosiberian birds but
13 not for Mediterranean species during the breeding season. Eurosiberian birds showed a
14 preference for more wooded habitats whereas Mediterranean birds preferred open
15 habitats and shrubland. Similarly, Sirami et al. (2008) found in eight localities of the
16 north-western Mediterranean Basin subjected to widespread land abandonment that
17 woodland and shrubland resident species showed the strongest increase, especially those
18 with a northern distribution, whereas migrants significantly decreased, especially
19 farmland species with a narrow habitat breadth.

20 In this study, we compared how two contrasting approaches of revegetation of
21 abandoned cropland in a Mediterranean system, namely passive vegetation restoration
22 or secondary succession and active vegetation restoration or tree plantations, affect bird
23 communities. These two contrasting trajectories of vegetation restoration depart from
24 recently abandoned cropland. Our main objective was to ascertain the effects of both
25 restoration trajectories on bird communities in agricultural landscapes by surveying bird

1 species and vegetation structure of stands under secondary succession or planted with
2 coniferous trees in central Spain. This study represents a direct comparison of the
3 effects of both types of restoration trajectories on bird communities. We hypothesized
4 that active restoration may negatively affect species that are characteristic of open
5 habitats and that portrait high conservation value in Europe, as reforestation with pines
6 creates a vegetation structure that is different from that present in natural Mediterranean
7 woodlands. We also studied whether the restored vegetation under these two contrasting
8 trajectories converge in their bird communities. These issues are relevant for
9 management of agricultural landscapes in a time when a variety of ecosystem goods and
10 services, and not just food and fiber production, are demanded from agrosystems. The
11 results of this study may thus provide useful guidelines to conciliate agricultural
12 production, restoration of native woodlands and bird conservation.

13

14 **2. Methods**

15 *2.1. Study area*

16 We surveyed bird communities in a ca. 6,000 km² area located in central Spain.
17 Extreme coordinates for the area are 41°00' N (North), 39°54' N (South), 3°46' W
18 (West) and 2°51' E (East). Altitude ranges between 631 and 1,008 m a.s.l. Climate in
19 this region is continental Mediterranean, with cold winters and warm dry summers.
20 Annual precipitation ranges between 436 mm in the lowest southern part and 598 mm in
21 the highest northern part, and mean annual temperature between 13 and 11 °C,
22 respectively. This region is included in the Mesomediterranean bioclimatic domain
23 (Rivas-Martínez, 1981). Bedrock is heterogeneous with dominance of chalkstone and
24 some extents of gypsum, granite and sandstone.

1 The mosaic of natural, semi-natural, introduced, and crop vegetation in the area
2 is a result of thousands of years of human exploitation. Natural vegetation chiefly
3 consists of evergreen forests dominated by holm oak, *Quercus rotundifolia*. The
4 degradation of these forests has led to more open woodland dominated by *Q.*
5 *rotundifolia*, *Juniperus oxycedrus*, or *Q. coccifera* or to shrubland dominated by *Cistus*
6 *ladanifer*, *Retama sphaerocarpa*, camephytes such as *Thymus* and *Lavandula* species,
7 and herbs (e.g. *Stipa* spp.). Large extents of land were reforested with pine species
8 (*Pinus halepensis* and *P. pinea*) after the 1950s and the eldest pine plantations are now
9 semi-natural forests (Peñuelas and Ocaña, 1996). Following subsidies from the
10 European Union, some cropland area was planted almost entirely with *P. halepensis*
11 after 1993. Thus, most afforested abandoned cropland ranges between 3 and 15 years in
12 age at the time we surveyed bird communities. The natural or semi-natural vegetation
13 and pine plantations intermingle with farmland mostly consisting of rain-fed cereals and
14 recently abandoned (<4 years old) cropland under secondary succession.

15

16 **2.2. Bird census**

17 Bird censuses were carried out during the breeding season (April 28th and June 1st) of
18 two consecutive years (2008–2009) by means of single-visit point-counts (Bibby et al.,
19 2000), ten min long each, recording all birds heard or seen within a 50-m radius plot.
20 Overflying birds were not considered. The censuses were conducted by the same two
21 well trained field technicians on windless and rainless days, between sunrise and 11 h
22 GMT in the morning. Point counts do not provide absolute densities, but relative
23 abundances. Nevertheless, the small area covered by the plots (0.78 ha), and the
24 relatively long time devoted to bird counts, maximizes the detection probability of
25 species and, thus, the accurate estimations of their abundance (Shiu and Lee, 2003).

1 Prior to sampling, we first explored the entire territory by means of aerial
2 photographs and Google Earth[®], and then visited the potential survey localities to locate
3 the census plots. A total number of 152 census plots were obtained in 48 localities
4 distributed throughout the study area in an attempt to sample the whole availability of
5 habitats and the altitude gradient (every plot was censused during only one year to
6 maximize a wide regional coverage). Of the 152 plots, 62 were located in stands under
7 woodland secondary succession, 75 in pine plantation stands, and 15 in recently (<4
8 years) abandoned cropland stands. Censuses of the different considered habitats were
9 spanned throughout the study period, avoiding censusing certain habitats in only one
10 year. We did not observe any clear inter-annual variation in bird abundance of the study
11 species, so we pooled all the censuses obtained in both years. The census plots were
12 geo-referenced with a portable GPS and separated at least 200 m from each other. They
13 were located in order to include homogeneous habitat types of the study area. These
14 main habitat types were abandoned cropland, pastureland, chamaephyte shrubland,
15 shrubland (mainly of genus *Cistus* and *Genista*), several stages of holm oak succession
16 to mature stands, and a range of afforested croplands with pines (from seedlings to pine
17 stands > 20 years old). These habitat types were used as a guideline to select the survey
18 localities.

19

20 ***2.3. Vegetation structure and NDVI***

21 Vegetation structure was sampled within a radius of 25-m centred in each census plot,
22 which was previously defined considering habitat homogeneity. This sampling was
23 carried out at the end of the bird census. We estimated by eye, after training, some
24 structural features of the habitat: percentage cover of bare soil, herbs, chamaephytes,
25 shrubs and trees, average height of chamaephytes, shrubs and trees, and number of

1 trunks 10-20, 21-40 and >40 cm in diameter at breast height or dbh (Table 1).
2 Vegetation cover was estimated according to the following percentage classes: 1 (0%),
3 2 (0.1%), 3 (0.5%), 4 (1%), 5 (1-5%), 6 (5-12.5%), 7 (12.5-25%), 8 (25-50%), 9 (50-
4 75%), 10 (75-90%), and 11 (>90%); we used the median values of these categories in
5 data analyses.

6 Finally, we also used a normalized difference vegetation index (NDVI) as a
7 radiometric index of photosynthetic activity (the larger the value, the more vigorous
8 vegetation). Raw data used to calculate this index were ten-day synthesis at 1 km²
9 spatial resolution captured by the MODIS Terra sensor (<https://wist.echo.nasa.gov/api/>)
10 for April-June of years 2006, 2007 and 2008. For each census plot we assigned the
11 maximum NDVI figure of the nine (3 months x 3 years) NDVI values recorded.

12

13 ***2.4. Species characteristics***

14 Regional patterns of distribution-abundance of the bird species detected in the 152 point
15 counts were summarized according to maximum density and habitat breadth of species
16 in the biogeographic region where the study area is included (Central Spain
17 Mesomediterranean region).

18 We estimated the maximum regional density (birds/km²) recorded in 13 major
19 habitat types of the study region as a measure of the maximum ecological abundance
20 that a species can attain in its most favorable environment. These 13 major
21 environments were established considering vegetation structure, floristic composition
22 and human impact and account for more than 95% of the surface of the whole study
23 area. They were the following: two types of urban environments (according to building
24 height and density), non-irrigated arable crops, irrigated arable crops, mixed orchards,
25 vineyards, olive plantations, two types of shrubland (according to shrub height and

1 density), pasturelands, pinewoods, deciduous woodlands and holm oak woodlands. The
2 data base for this analysis was obtained from the Spanish SACRE program (monitoring
3 of common breeding birds in Spain), using 3,417 five-min point-counts censused in
4 years 2004, 2005 and 2006, and distributed over the study area. Absolute densities for
5 this data base were obtained using detectability provided by Carrascal and Palomino
6 (2008) of the same census program.

7 Regional habitat breadth of species in the above mentioned 13 major habitat
8 types was calculated following the Levins' (1968) index divided by the number of
9 habitat categories:

$$10 \quad \text{HB} = [(\sum p_i^2) - 1] / 13$$

11 where p_i is the proportion of the density for each species measured in the habitat i
12 (dividing density in habitat i by the sum of all maximum densities recorded in the 13
13 habitat categories). This index ranges between 1 (evenly distributed across the 13
14 habitats) and 1/13 (only present in one habitat).

15 Bird species were included into five ornitogeographical groups according to
16 Voous (1960): Holarctic-Palearctic, European (*sensu lato*), Mediterranean (*sensu lato*),
17 and other two minor and rare groups in the study area (Ethiopic, and Old World).

18 Finally, we also looked at the relative abundances (average bird counts per
19 census plot) of bird species in recently abandoned cropland stands and in the most
20 mature holm oak woodland (i.e. corresponding to secondary succession) and pine
21 plantation stands (15 stands of each trajectory).

22

23 **2.5. Data analyses**

24 Bird species richness was estimated as the total number of species detected in each
25 census plot. Bird species composition was summarized by means of a Principal

1 Coordinate Analysis (PCORD) on presence-absence data of the most common bird
2 species (i.e. 19 species present in more than 5% of the census plots). Only the first
3 component of the compositional gradient was considered in further analyses.

4 The average of the maximum regional density and of the regional habitat breadth
5 in the study region of bird species in each census plot was calculated by means of the
6 weighted averages of these figures for each species, using species counts in each plot as
7 weights.

8 The relationships between the response variables (bird species richness,
9 assemblage composition, and weighted averages of maximum regional density –in
10 logarithm- and regional habitat breadth) and vegetation structure variables (predictors)
11 were analysed by means of Partial Least Squares Regressions (hereafter PLSR; Swold
12 et al., 2001; Tobias, 2003), using census plots as sample units. This statistical tool is an
13 extension of multiple regression analysis where associations are established with factors
14 extracted from predictor variables that maximize the explained variance in the
15 dependent variable. These factors are defined as a linear combination of independent
16 variables, so the original multidimensionality is reduced to a lower number of
17 orthogonal factors to detect structure in the relationships between predictor variables
18 and between these factors and the response variable. The extracted factors account for
19 successively lower proportions of original variance. The relative contribution of each
20 variable to the derived factors was calculated by means of the square of predictor
21 weights. Results obtained with PLSR are similar to those from conventional multiple
22 regression techniques; however, it is extremely robust to the effects of sample size and
23 degree of correlation between predictor variables, which makes PLSR especially useful
24 when sample size is low and in cases of severe multicollinearity (Carrascal et al., 2009).

1 One-way ANCOVAs were then used to test whether the response variables
2 differed between passive (i.e. woodland secondary succession) or active (i.e. pine
3 plantations) restoration trajectories (fixed factor) while controlling for vegetation
4 structure of the census plots using the scores of the first PLSR axis as covariate. The
5 interaction term vegetation structure (i.e. PLSR scores) \times type of restoration trajectory
6 was also estimated to explore possible differences between restoration trajectories in the
7 avian response to vegetation structure. Residuals of PLSR and ANCOVA models were
8 checked to fulfill normality.

9

10 **3. RESULTS**

11 *3.1. Vegetation structure*

12 Most variables of vegetation structure at census plots differed in the two contrasting
13 trajectories of vegetation restoration, i.e. secondary succession and pine plantations
14 (Table 1). There was a larger development of the tree layer and more amount of bare
15 soil in the pine plantations than in the secondary shrubland and holm oak woodlands.
16 However, understory layers attained higher cover values in the latter. NDVI and cover
17 of the herbaceous layer were similar at both restoration trajectories. Most mature
18 woodland stands averaged a tree height of 4 m and a tree cover of 45%, whereas these
19 structural variables averaged 9.2 m and 57%, respectively, in the most mature pine
20 plantations.

21

22 *3.2. Effects of vegetation restoration on bird species richness and composition*

23 *Species richness.* The PLSR carried out with the 152 census plots provided a first
24 component explaining 20.6% of variance in bird species richness (Table 2). This

1 component related species richness positively to tree cover and height and to the
2 number of thin and medium-sized trunks (10-40 cm dbh), and negatively to
3 chamaephyte height (Table 2). Thus, bird species richness increased with development
4 of the tree layer (Figure 1).

5 An ANCOVA model performed with species richness as the response variable,
6 type of restoration as categorical factor, and the scores of the first PLSR component of
7 vegetation structure variables as covariate, showed that species richness was
8 significantly higher at the active restoration trajectory than at the passive restoration
9 trajectory ($F_{1, 134} = 4.28$, $P = 0.04$). The adjusted means (controlling for the PLSR
10 component) were 4.2 species per 0.78 ha plot in pine plantations and 3.5 species per
11 plot in secondary shrublands and woodlands (Figure 2A). The interaction term
12 vegetation structure \times type of restoration trajectory was not significant ($F_{1, 133} = 0.47$, P
13 $= 0.496$).

14

15 **Species composition.** The principal coordinate analysis (PCORD) with species
16 occurrence in the 152 plots provided a first composition component strongly and
17 positively correlated with the presence of generalist bird species preferring arboreal
18 habitats (*Fringilla coelebs*, *Serinus serinus*, *Parus major*, *Cyanistes caeruleus*,
19 *Carduelis chloris* and *Carduelis carduelis*), and negatively correlated with the presence
20 of open habitat species (*Sylvia melanocephala*, *Sylvia undata*, *Alectoris rufa*, *Emberiza*
21 *calandra* and *Galerida cristata*). The variation explained by this component was 18.6%,
22 and it was associated with the dominant, more widely distributed species.

23 The PLSR analysis accounted for 58.6% of inter-plot variation in bird species
24 composition. The PLSR component was strongly and positively related to tree layer

1 development (tree cover and average height and density of thin and medium sized
2 trunks) and negatively associated with development of the chamaephyte layer (Table 2).

3 The effect of restoration trajectory significantly influenced bird species
4 composition (different slopes ANCOVA, $F_{1, 133} = 5.29$, $P = 0.023$); the occurrence of
5 generalist woodland bird species was higher in pine plantations than in secondary
6 shrublands and woodlands (Figure 2B). The interaction term vegetation structure \times type
7 of restoration trajectory revealed a significant inter-plot variation in bird species
8 composition ($F_{1, 133} = 6.26$, $P = 0.013$) with development of the tree layer, i.e. stands
9 under active restoration showed a strongest association between species composition
10 and habitat maturity. Generalist bird species preferring arboreal habitats had a higher
11 occurrence in pine plantations than in secondary shrublands and woodlands (Figure 3).

13 *3.3. Effects of vegetation restoration on distribution-abundance features of bird* 14 *species*

15 **Maximum regional density.** A PLSR generated a component explaining 12.2% of
16 variance in the maximum regional density of birds. Bird assemblages inhabiting areas
17 with a well developed herbaceous layer and a low cover of chamaephytes and shrubs,
18 irrespective of the tree layer development (see the very low weights of vegetation
19 variables describing the tree layer in Table 2), were dominated by species which
20 attained highest maximum density at the regional level.

21 An ANCOVA model provided a significant interaction term vegetation structure
22 \times type of restoration trajectory ($F_{1, 129} = 4.11$, $P = 0.045$; four census plots were treated
23 as missing values because no species were recorded during bird censuses, and thus a
24 weighted averaged by bird counts made no sense). Maximum regional density did not
25 differ between both restoration trajectories (different slopes ANCOVA, $F_{1, 129} = 0.004$,

1 $P = 0.948$; Figure 2C). The slope of the regression between maximum regional density
2 and the scores of the PLSR component was only significantly different from zero in the
3 case of stands under passive restoration (secondary succession slope = 0.33, $P < 0.001$),
4 but not in stands under active restoration (pine plantation's slope = 0.10, $P = 0.159$,
5 Figure 4). Thus, local occurrence of bird species that were very abundant in their
6 preferred habitats at the regional scale was negatively linked to the development of the
7 camephyte-shrub layer and increased with development of the herbaceous layer only at
8 the secondary succession trajectory. Maximum regional density of each species is
9 reported in the Appendix.

10

11 ***Regional habitat breadth.*** A PLSR analysis generated a vegetation structure component
12 accounting for 22.8% of variance in regional habitat breadth of bird species occurring in
13 census plots. Regional habitat breadth was negatively related to NDVI, shrub layer
14 development (vegetation cover and height), and tree height and density of medium-sized
15 trunks; Table 2). That is to say, habitat generalists at the regional scale are mainly
16 linked to relatively low biomass habitats, avoiding more vegetated areas covered with
17 growing vegetation generated by secondary succession or pine plantations.

18 An ANCOVA model found marked differences between the two restoration
19 trajectories ($F_{1, 130} = 11.86$, $P < 0.001$; Figure 2D). Bird species inhabiting pine
20 plantations had, on average, broader habitat preferences at the regional level than those
21 inhabiting the secondary shrublands and woodlands. The interaction between vegetation
22 structure \times type of restoration trajectory was not significant ($F_{1, 129} = 0.146$, $P = 0.703$;
23 four census plots were treated as missing values because no species were recorded
24 during bird censuses, and thus a weighted averaged by bird counts made no sense).
25 Regional habitat breadth of each species is reported in the Appendix.

1

2 ***3.4. Bird density and biogeographic origin in contrasted restoration scenarios***

3 Average bird density was 32.3 birds/10 ha in recently abandoned cropland stands, 66.3
4 birds/10 ha in the 15 most mature holm oak woodland stands, and 118.3 birds/10 ha in
5 the 15 most mature pine plantation stands that were censused (Appendix). Bird
6 abundance of species of European biogeographic origin attained 58.9% of total bird
7 abundance in mature pine plantations, while these figures were lower in mature holm
8 oak woodlands (34.4%) and recently abandoned cropland (37.8%). Conversely, the
9 relative importance of Mediterranean species was considerably higher in mature holm
10 oak woodlands (40.1%) than in the two other habitat types (ca. 20%). Finally, species
11 with Holarctic-Palearctic distribution were relatively more important in recently
12 abandoned cropland (37.2%) than in mature holm oak woodlands or pine plantations
13 (ca. 22%).

14

15

16 **4. Discussion**

17

18 ***4.1. Structure of restored vegetation after cropland abandonment***

19 The identified trajectories of vegetation restoration have led to a mosaic of small
20 patches of semi-natural vegetation in a ‘sea’ of croplands in the studied area. Tree
21 plantations focused on pine species, and thus their vegetation structure is clearly
22 different than that of evergreen secondary shrubland and woodland dominated by *Q.*
23 *rotundifolia* and accompanying species. This marked difference between the two
24 restoration trajectories is mainly determined by the larger development of the tree layer

1 in the pine plantations due to faster growth of pines than holm oaks (Broncano et al.,
2 1998). However, in spite of similar “quantity of vegetation” as measured by remote
3 sensing NDVI, vertical development of vegetation structure is clearly more complex in
4 the studied secondary succession stands than in pine plantation stands, as understory
5 layers attain higher cover values in the former but bare soil cover is higher and a
6 monotonous tree crown dominates in the latter (Table 1). Other studies have reported
7 similar results to our findings (Pausas et al., 2004; Ruiz-Jaen and Aide, 2005).

8

9 ***4.2. Bird species composition and habitat breadth***

10 The effects of landscape changes on bird assemblages are the consequence of their
11 magnitude combined with adaptations that species have been able to achieve to face
12 with such changes during their history (see Blondel, 1990 and Covas and Blondel, 1998
13 for forest avifauna in the Mediterranean region). We highlighted that bird species
14 composition differs in stands under passive or active restoration trajectory, the latter
15 collecting more species that inhabit forested habitats than the former. Conversely, pine
16 plantations are not permeable to some Mediterranean species such as *Sylvia*
17 *melanocephala*, *S. undata*, *S. cantillans*, *Lanius senator*, and *Alectoris rufa*; which
18 attain highest densities in the slow growing holm oak secondary succession trajectory
19 (Brotons and Herrando, 2001; Sirami et al., 2008; Gil-Tena et al., 2009). The
20 degradation of evergreen forests dominated by *Q. rotundifolia* as a consequence of
21 human activities during thousands of years has led to more open woodlands or to
22 shrublands, and thus bird assemblages in Spanish Mediterranean forests currently
23 present a high proportion of species that inhabit more open habitats and only a small
24 proportion of true forest birds (Santos et al., 2002). We also found that the capacity of
25 pine plantations to collect forest birds is more dependent on the structural characteristics

1 of vegetation than passively restored stands. Therefore, the benefits to forest birds of
2 pine plantations in our study area are only fulfilled by tree plantations with highly
3 mature vegetation (i.e. the oldest ones; see Figure 3).

4 High habitat breadth is frequent in species that are common and tolerate a
5 relatively wide range of ecological conditions (Hurlbert and White, 2007; Carrascal and
6 Seoane, 2008). Accordingly, regional habitat breadth of species in our study increases
7 with vegetation complexity, as the vegetation of stands under passive or active forest
8 restoration grows in the 'sea' of croplands. Only generalist woodland species, with large
9 habitat breadth at the regional level such as *Fringilla coelebs*, *Carduelis carduelis*, *C.*
10 *chloris*, *Parus major* and *Turdus merula*, are able to occupy the small woodland stands
11 indistinctly of the type of restoration trajectory. Conversely, more specialized forest bird
12 species, such as *Loxia curvirostra*, *Sitta europaea*, *Periparus ater*, *Lophophanes*
13 *cristatus*, *Erithacus rubecula*, and *Regulus ignicapillus* are very scarce in the surveyed
14 woodland stands (see Appendix), as they are restricted to mature stands in large forest
15 tracts outside the study region (the nearest areas are located in the mountain ranges of
16 the Supramediterranean bioclimatic region in Central Spain). These results are in
17 agreement with previous studies (Sirami *et al.* 2008).

18

19 **4.3. Bird species richness and regional density**

20 Tree growth under passive or active restoration trajectory positively affected both bird
21 species richness and regional density. The influence of the passive or active vegetation
22 restoration after cropland abandonment in this region is consistent with the pattern of
23 relationships between bird communities and the increase in structural complexity of
24 growing vegetation that is observed worldwide (Wiens 1989, Nájera and Simonetti
25 2009). Nevertheless, this positive effect was considerable higher in pine plantations than

1 in the secondary succession trajectory, and is mainly related to the ubiquitous presence
2 of generalist woodland species in the plantations. However, Díaz et al. (1998) and
3 Maestre and Cortina (2004) found a reduction in bird diversity in pine plantations as
4 compared to evergreen woodlands.

5 The fragmented character of growing woodland patches as a result of secondary
6 succession or pine plantations is actually constraining the increase of species richness in
7 the breeding bird communities of the Mediterranean region (Díaz et al. 1998, Brotons
8 and Herrando 2001). Tellería et al. (2003) have proposed that the relationship between
9 regional richness of forest birds and richness in fragments seem to explain why
10 fragments in southern Europe shelter fewer species than in central and northern
11 European latitudes. These authors have also shown that the decreased ability of southern
12 forest fragments to sample the regional richness of forest birds could be explained as an
13 effect of the low abundance of many species in the Mediterranean, which could depress
14 their ability to prevent extinction in fragments by a rescue effect. In a nearby region of
15 the Spanish plateau, Díaz et al. (1998) found that plantations smaller than 25 ha only
16 maintained 50% of the regional pool of forest birds during the breeding season.

17

18 ***4.4. Biogeographic origin and bird species richness***

19 The increase in species richness has a different meaning according to the biogeographic
20 origin of bird species. Pine plantations “capture” more species with European or
21 Euroturkestan distribution patterns (Voous, 1960) than the secondary succession
22 trajectory, while holm oak woodlands are composed by a larger proportion of bird
23 species with a Mediterranean distribution pattern. These differences are related to past
24 climatic events influencing the avifauna of the western Palearctic (Blondel and Farré,
25 1988; Blondel and Mourer-Chauviré, 1998; Mönkkönen, 1994). In the Iberian

1 Peninsula, the patterns of geographic distribution and environmental preferences of
2 woodland birds reflect the distribution patterns at broader geographic scales (the
3 southwestern Palearctic region; Carrascal and Díaz 2003). Moreover, the single climatic
4 variable number of cloudless days per year was the most important variable negatively
5 affecting the geography of species richness for bird species with European and
6 Palearctic distribution pattern, while the mountainous character of areas positively
7 affected species richness of these ornitogeographical groups. Conversely, woodland
8 species with core biogeographic areas located in the Mediterranean basin are more
9 frequent in the Iberian Peninsula in warm valleys, covered with little forest extent and
10 large extensions of wooded agricultural formations (Carrascal and Díaz 2003; see also
11 Moreno-Rueda and Pizarro, 2008 for the effect of temperature on these biogeographic
12 groups of bird species). At local scales, Mediterranean bird species are restricted to the
13 early stages of succession and are replaced by temperate forest species as succession
14 progresses on (Preiss et al., 1997).

15

16 ***4.5. Conservation and concluding remarks***

17 Habitat changes induced by cropland abandonment are expected to be critical at
18 determining future biodiversity patterns in large areas of the Mediterranean Basin
19 (Preiss et al., 1997; Herrando et al., 2003; Sirami et al., 2007; Vallecillo et al., 2008).
20 These changes, may be especially detrimental for several open habitat species with
21 declining populations at both the European (Gregory et al., 2005) and the Iberian
22 Peninsula levels (Carrascal and Palomino, 2008; Seoane and Carrascal, 2007), which
23 are of particular conservation concern (Tucker and Heath, 1994; BirdLife International,
24 2004). Thus, when pine afforestation is not possible to impede, fewer but larger

1 afforested patches rather than numerous and smaller patches scattered across the
2 landscape may be preferable.

3 We did not sample any species threatened with extinction. We sampled species
4 such as *Alectoris rufa* and *Lanius senator*, with an unfavourable conservation status in
5 Europe, which tend to be more abundant in passively restored stands than in actively
6 restored stands, making the habitat provided by secondary succession of importance for
7 species conservation. Since pine plantations do not attract bird species that present high
8 habitat breadth and density, these relatively small and new habitat patches are unable to
9 foster the assemblages of birds that are found at a regional scale. Thus, patches of pine
10 plantations are not similar to patches of isolated natural forests regarding the capacity to
11 foster bird assemblages, as relationships between local and regional bird communities
12 seem to be only observed in the latter (van Dorp and Opdam, 1987).

13 We identified two major trajectories of vegetation restoration in Mediterranean
14 abandoned cropland that markedly differ in vegetation complexity and associated bird
15 assemblages. Pine plantations increased local bird species richness as they favored
16 several Palearctic, Holarctic and European species, which chiefly are generalist
17 woodland species. However, they failed to capture a representative pool of species from
18 the regional avifauna, and hence are unlikely to enhance regional biodiversity of
19 woodland birds (Díaz et al., 1998). Secondary succession provided more favorable
20 habitats for species of conservation concern in the European context. Since passively
21 and actively restored stands favored different bird species, any extensive and
22 conventional forestry based on coniferous trees are improbable to be successful in
23 conserving bird communities that inhabit complex Mediterranean mosaics of open
24 habitats and forest ecosystems (Artman 2003, Carey 2003, Thompson et al. 2003, Hagar
25 et al. 2004). Thus, programs of vegetation restoration should base upon a range of

1 approaches that include passive restoration, active restoration with a variety of tree and
2 shrub species native to the particular region and mixed models such as the woodland
3 islets in agricultural seas (Rey Benayas et al., 2008) and others (e.g. Munro et al., 2010),
4 which are capable of conciliating agricultural production, vegetation restoration and
5 conservation of target species.

6

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12

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12

1 **Figure 1.** Relationship between bird species richness and a vegetation structure PLSR
2 component (positively related to tree layer development and negatively associated with
3 camephyte height; see Table 2) in the holm oak secondary succession trajectory (open
4 circles) and pine plantation trajectory (solid symbols). The horizontal dashed line
5 represents the average species richness in recently abandoned croplands (n=15).

6

7 **Figure 2.** Bird species richness (A), composition (B; principal coordinate component),
8 maximum regional density (C) and regional habitat breadth (D) of bird assemblages in
9 stands of Central Spain in the holm oak secondary succession trajectory and pine
10 plantation trajectory. Bars denote adjusted means \pm one standard error from GLMs
11 including the PLSR vegetation component (see Methods).

12

13 **Figure 3.** Relationship between a principal coordinate component of bird species
14 composition (opposing woodland generalists to open habitat bird species) and a
15 vegetation structure PLSR component (positively related to tree layer development and
16 negatively associated with camephyte height; see Table 2) in the holm oak secondary
17 succession trajectory (open circles and dashed line) or pine plantation trajectory (solid
18 symbols and continuous lines).

19

20 **Figure 4.** Relationship between maximum regional density of bird assemblages and a
21 vegetation structure PLSR component (increase in herbaceous cover with decreasing
22 cover of camephyte and shrubs; see Table 2) in the holm oak secondary succession
23 trajectory (open circles and dashed line) or pine plantation trajectory (solid symbols and
24 continuous lines).

25

1 **Appendix.**

2

3 Average density of bird species in census plots (50 m radius; birds / 10 ha). RAC:

4 recently abandoned crops (<4 years old; n=15); HOLMOAK-W: mature holm oak

5 woodlands (n=22 census plots; average tree height > 3 m); PINE-P: mature pine

6 plantations (n=38; average pine height > 3 m). BDP: biogeographic distribution patterns

7 according to Voous (1960; HP: Holarctic or Palearctic; E: European or Euroturkestan;

8 M: Mediterranean s.l.; OW: Old World; ETH: Ethiopic). DMAX: maximum density

9 recorded at the regional level in 13 major habitat types (in bird / 10 ha). HB: habitat

10 breadth at the regional level in 13 major habitat types.

11

	BDP	RAC	HOLMOAK-W	PINE-P	DMAX	HB
<i>Aegithalos caudatus</i>	HP	0.0	2.3	6.0	4.2	0.30
<i>Alauda arvensis</i>	HP	3.2	0.0	0.0	0.7	0.49
<i>Alectoris rufa</i>	M	0.6	0.6	0.0	5.8	0.79
<i>Carduelis cannabina</i>	E	1.3	0.6	2.0	6.9	0.81
<i>Carduelis carduelis</i>	E	4.5	0.0	17.8	16.2	0.83
<i>Carduelis chloris</i>	E	0.0	1.2	5.7	11.3	0.69
<i>Certhia brachydactyla</i>	E	0.0	0.0	0.7	3.0	0.53
<i>Columba palumbus</i>	E	0.0	1.2	4.0	9.5	0.81
<i>Coturnix coturnix</i>	OW	0.6	0.0	0.0	0.3	0.52
<i>Cuculus canorus</i>	HP	0.0	0.0	0.3	1.1	0.54
<i>Dendrocopos major</i>	HP	0.0	0.6	0.7	0.2	0.45
<i>Emberiza calandra</i>	E	6.4	1.7	0.7	11.0	0.73
<i>Emberiza cia</i>	HP	0.0	0.0	0.3	1.8	0.38
<i>Erithacus rubecula</i>	E	0.0	0.6	0.3	3.0	0.32
<i>Fringilla coelebs</i>	E	0.0	8.7	28.1	10.1	0.55
<i>Galerida cristata</i>	HP	7.0	0.6	0.0	20.6	0.71
<i>Galerida theklae</i>	M	1.3	0.0	1.3	2.2	0.60
<i>Garrulus glandarius</i>	HP	0.0	0.0	0.3	0.8	0.47
<i>Hirundo daurica</i>	IA	0.0	0.6	0.0	1.4	0.73
<i>Lanius meridionalis</i>	M	0.0	0.6	0.0	0.6	0.63
<i>Lanius senator</i>	M	0.6	0.6	0.0	2.9	0.51
<i>Loxia curvirostra</i>	HP	0.0	0.0	1.3	0.2	0.08
<i>Lullula arborea</i>	E	0.0	0.6	0.3	2.6	0.38
<i>Luscinia megarhynchos</i>	E	0.0	1.7	0.3	8.2	0.61
<i>Periparus ater</i>	HP	0.0	0.0	1.7	4.3	0.24
<i>Cyanistes caeruleus</i>	E	0.0	4.1	2.3	7.4	0.57

<i>Lophophanes cristatus</i>	E	0.0	0.0	3.4	2.2	0.22
<i>Parus major</i>	HP	0.0	2.9	7.7	6.4	0.66
<i>Passer domesticus</i>	HP	0.6	0.6	0.7	180.3	0.61
<i>Phylloscopus bonelli</i>	E	0.0	0.0	0.7	3.3	0.26
<i>Pica pica</i>	HP	0.6	8.7	3.0	7.0	0.84
<i>Picus viridis</i>	E	0.0	0.6	0.7	0.3	0.77
<i>Regulus ignicapillus</i>	E	0.0	1.2	1.0	2.3	0.17
<i>Serinus serinus</i>	M	2.5	4.6	20.4	19.5	0.68
<i>Sitta europaea</i>	HP	0.0	0.0	0.3	0.3	0.26
<i>Streptopelia turtur</i>	E	0.0	0.6	0.0	1.9	0.56
<i>Sturnus unicolor</i>	M	0.0	0.0	0.3	39.7	0.85
<i>Sylvia atricapilla</i>	E	0.0	0.0	1.0	2.2	0.47
<i>Sylvia cantillans</i>	M	0.0	2.3	0.0	5.4	0.36
<i>Sylvia melanocephala</i>	M	2.5	15.0	1.0	6.4	0.41
<i>Sylvia undata</i>	M	0.0	2.9	0.3	0.4	0.66
<i>Turdus merula</i>	HP	0.6	0.6	3.0	8.8	0.72
<i>Turdus viscivorus</i>	E	0.0	0.0	0.7	0.8	0.25
<i>Upupa epops</i>	ETH	0.0	0.6	0.0	1.1	0.73

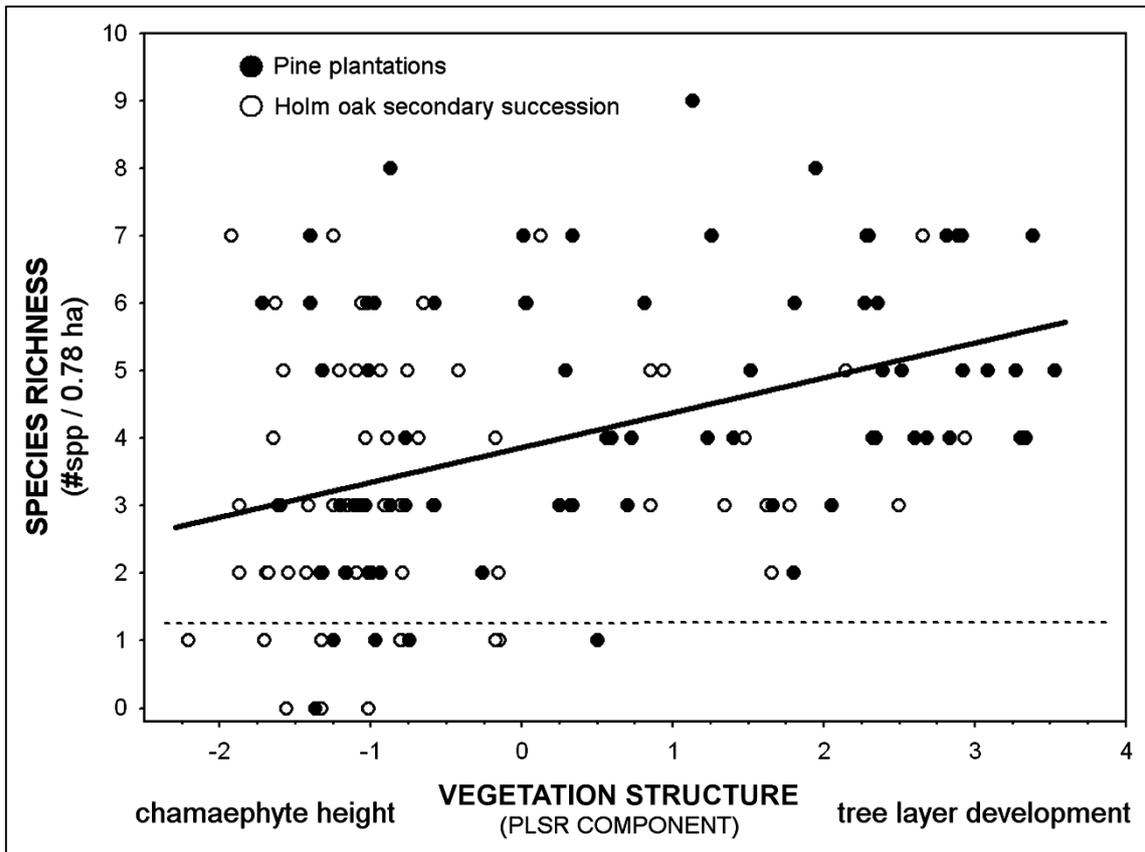


Fig. 1

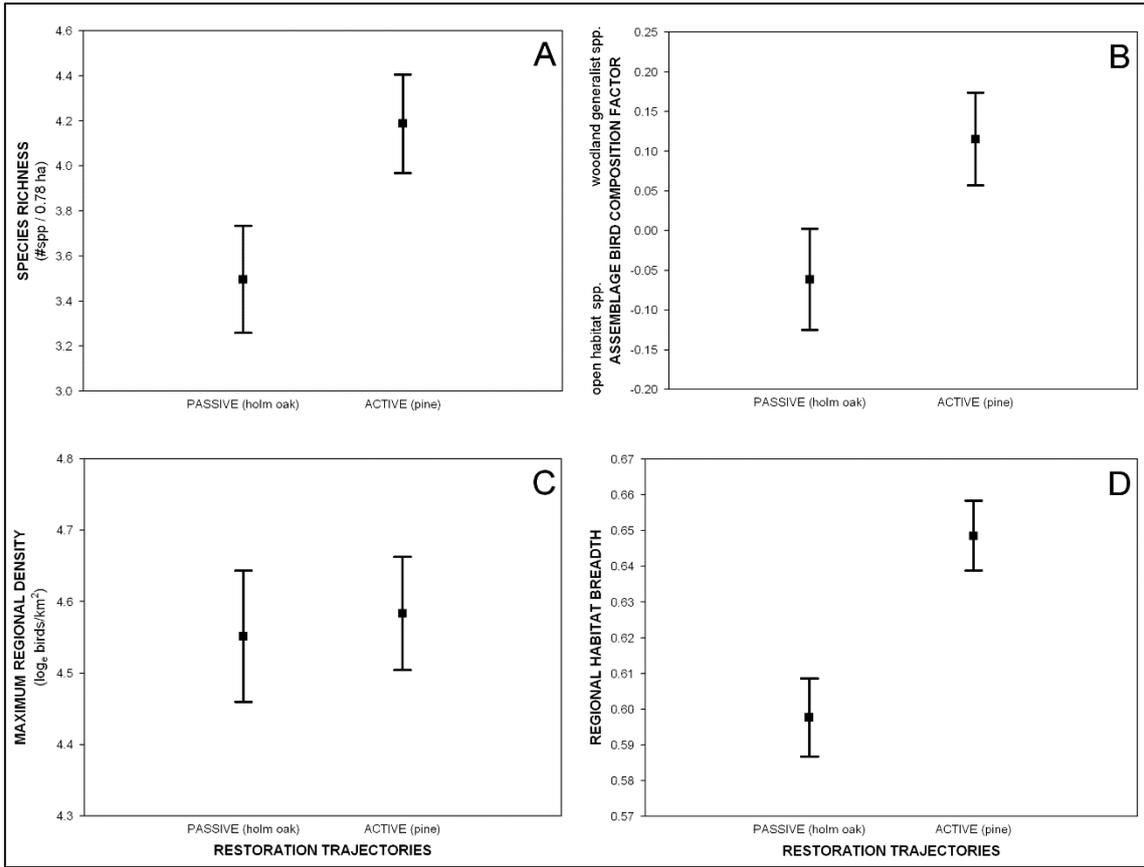


Fig. 2

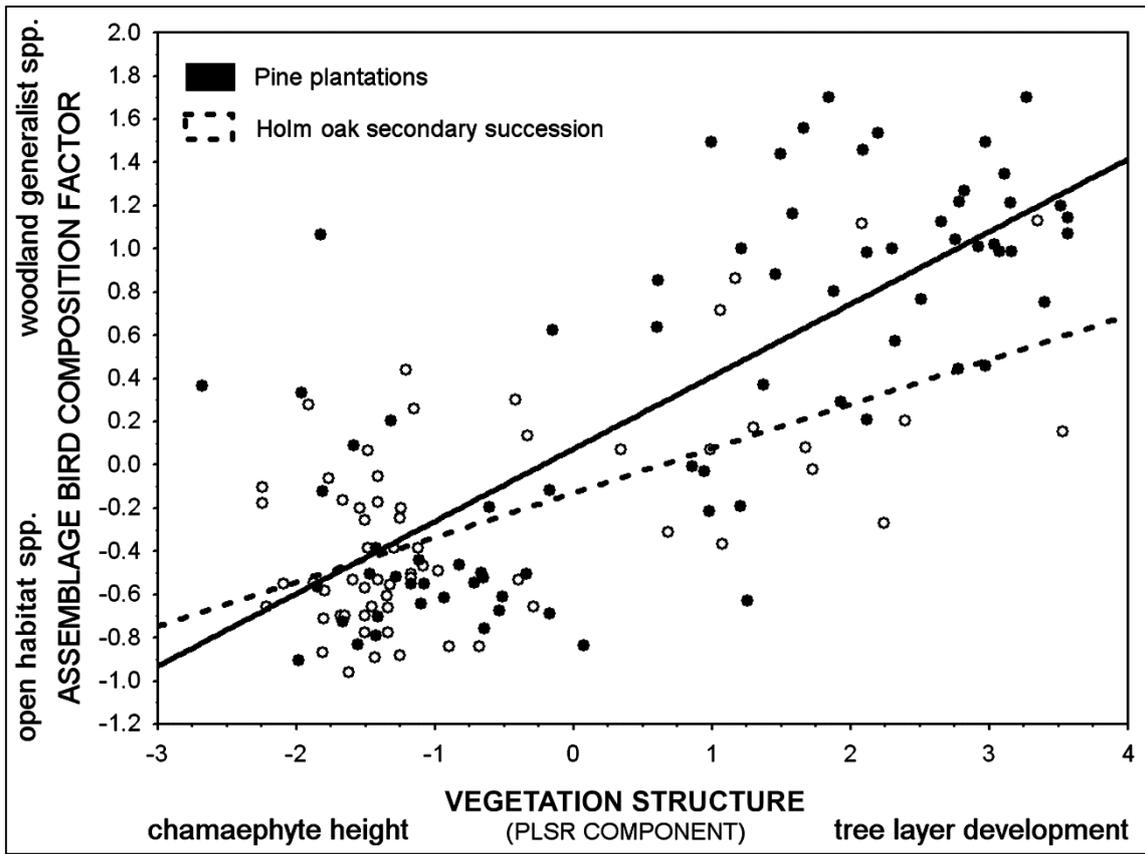


Fig. 3

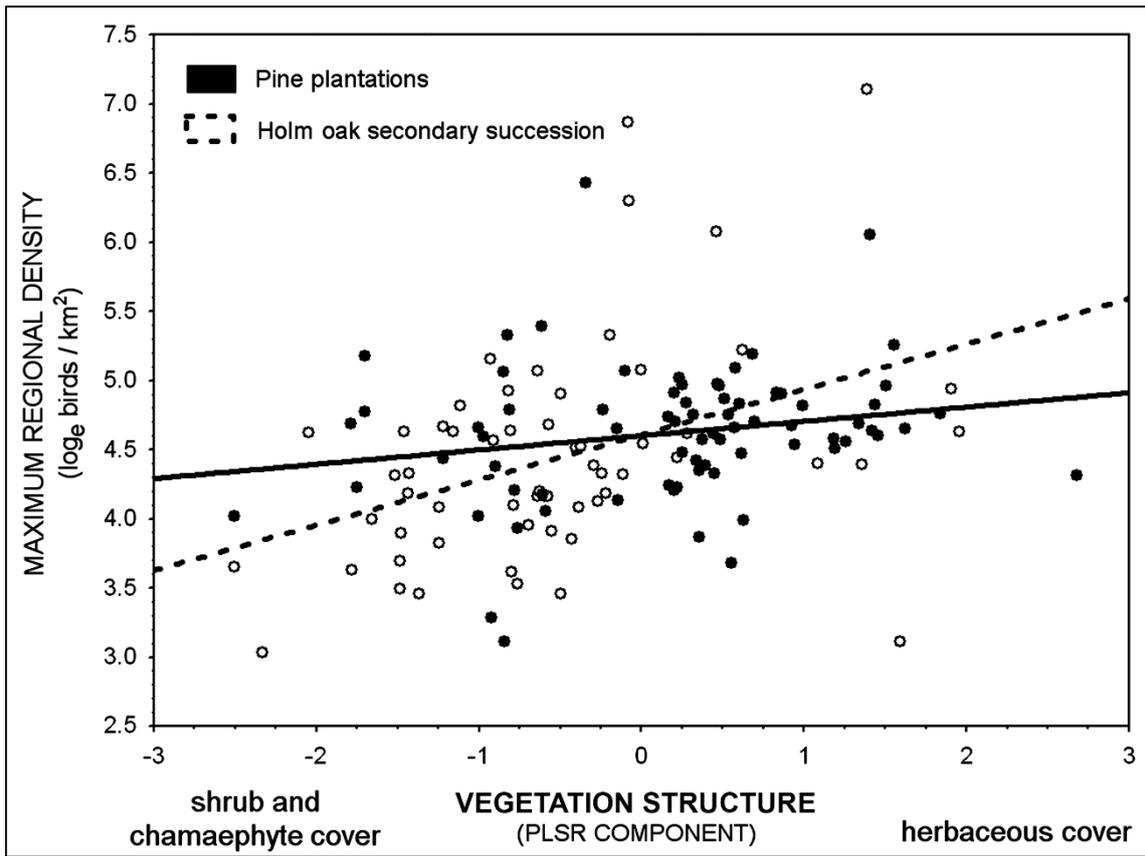


Fig. 4

1 **Table 1.** Structural characteristics of census plots in two contrasting trajectories of
 2 vegetation restoration in agricultural landscapes of Central Spain. Mean, ranges (min –
 3 max) and *P*-value according to Mann-Whitney tests for each variable are reported.

	PASSIVE RESTORATION (secondary succession; n=62)	ACTIVE RESTORATION (pine plantations; n=75)	P
NDVI	0.50 (0.29 – 0.65)	0.48 (0.27 – 0.67)	0.216
Bare soil cover (%)	32 (0 – 62)	57 (0 – 95)	<0.0001
Herbaceous layer cover (%)	23 (0 – 95)	22 (0 – 95)	0.859
Chamaephyte cover (%)	14 (0 – 82)	10 (0 – 62)	0.013
Shrub cover (%)	27 (0 – 62)	13 (0 – 82)	<0.0001
Tree cover (%)	10 (0 – 62)	31 (0 – 82)	<0.0001
Mean chamaephyte height (m)	0.24 (0 - 0.7)	0.13 (0 - 0.5)	0.002
Mean shrub height (m)	1.2 (0 - 2.8)	1.0 (0 – 2.8)	0.163
Mean tree height (m)	1.4 (0 – 6)	4.1 (0 – 12)	0.0001
No. trunks 10-20 cm dbh	72 (0 – 781)	44 (0 – 184)	0.002
No. trunks 21-40 cm dbh	2.6 (0 – 38)	5.4 (0 – 59)	0.03
No. trunks > 40 cm dbh	0.2 (0 – 13)	0.5 (0 – 18)	0.809

Table 2. Predictor weights of the four Partial Least Squares Regression (PLSR) analyses explaining the relationship between species richness, a component of species composition, maximum regional density, and regional habitat breadth of birds (response variables) and structural features of vegetation (predictor variables) in stands of Central Spain under either passive or active restoration trajectories. Predictor weights represent the contribution of each vegetation variable to the PLSR axis. Predictor weights explaining more than 5% of the total variance in each response variable are shown in bold type.

Predictor variables	Species richness	Species composition	Maximum regional density	Regional habitat breadth
NDVI (0-255)	0.16	0.13	-0.14	-0.35
Bare soil cover (%)	0.09	0.20	0.11	0.29
Herbaceous layer cover (%)	-0.16	-0.03	0.63	0.20
Chamaephyte cover (%)	0.10	-0.16	-0.44	0.14
Shrub cover (%)	0.02	-0.20	-0.52	-0.62
Tree cover (%)	0.61	0.57	0.05	-0.10
Mean chamaephyte height (m)	-0.25	-0.25	0.04	-0.00
Mean shrub height (m)	0.05	-0.07	0.08	-0.39
Mean tree height (m)	0.60	0.56	0.06	-0.32
No. trunks 10-20 cm dbh	0.28	0.25	-0.20	-0.00
No. trunks 21-40 cm dbh	0.25	0.31	0.05	-0.23
No. trunks > 40 cm dbh	-0.03	0.06	0.22	-0.21
% variance accounted for	20.6	58.6	12.2	22.8