Regional distribution predicts bird occurrence in Mediterranean cropland afforestations

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Abstract Part of the abandoned cropland in Mediterranean landscapes is being subjected to afforestation dominated by pines. Here we simultaneously evaluate the effect of three categories of factors as predictors of the interspecific variation in bird habitat occupancy of fragmented afforestations, namely regional distribution, habitat preferences and life history traits of species. We use the "natural experiment" that highly fragmented pine plantations of Central Spain represent due to the prevailing pattern of land ownership of small properties. Many species with marked habitat preferences for woodland habitats were very scarce or were never recorded in this novel habitat within a matrix of deforested agricultural landscape. Interspecific variability in occurrence was mainly explained by regional distribution patterns: occurrence was significantly and positively associated with the proportion of occupied 10x10 UTM km squares around the study area, regional habitat breadth, and population trend of species in the period 1998-2011. It was also positively associated with regional occupancy of mature and large pine plantations. Other predictor variables related to habitat preferences (for woodland, agricultural and urban habitats) or life history traits (migratory strategy, body mass and clutch size) were unrelated to the occurrence of species. Thus, small man-made pinewood islands funded by the Common Agrarian Policy (CAP) within a landscape dominated by Mediterranean agricultural habitats only capture widespread and habitat generalist avian species with increasing population trends, not contributing to enhance truly woodland species.

Keywords Bird occurrence · Cropland abandonment · Habitat preferences · Pine plantations · Regional distribution

Introduction

Afforestation represents a strategy to produce forest land on abandoned cropland that avoids the long time that secondary succession usually takes, particularly in the drylands of the world (Rey Benayas and Bullock 2012). In the European Union, the Common Agrarian Policy (CAP) has favoured the transformation of farmland into tree plantations since 1992 by means of a scheme of aid for forestry measures in agriculture (EEC Council Regulation No. 2080/92), which has resulted on the afforestation of ca. 921,210 ha to date (Directorate-General for Agriculture and Rural Development 2012). These afforested fields, which in southern Europe are mostly based on coniferous species such as *Pinus halepensis* and *P. pinaster*, usually form an archipelago of habitat patches in the dominant agricultural matrix (Izhaki 1999; van Meijl et al. 2006). These afforestations impact on biodiversity because pine plantations have higher tree cover and less structural heterogeneity than natural Mediterranean woodlands (Sirami et al. 2007; Rey Benayas et al. 2010).

Birds represent the group of vertebrates upon which these impacts have been most intensively studied, and are good indicators of the success of colonization of these afforestations because they are highly mobile animals that easily reach these novel ecosystems. It is widely known that the age, area and habitat structure of woodland islands are tightly related to species richness and bird community composition of pine plantations (e.g. Díaz et al. 1998; Shochat et al. 2001). Nevertheless, little is known about the filtering processes determining the identity of species occupying pine plantations within the regional pool of species in Mediterranean landscapes dominated by agricultural habitats. Three major types of effects may determine bird species identity in Mediterranean cropland afforestations, namely regional distribution patterns, habitat preferences of species and autoecological traits related to life history. Species with high density are more likely to be included in habitat fragments than scarce ones as a consequence of their abundance (Connor and McCoy 1979; Andrén 1999), and thus bird communities inhabiting afforested fields would represent random subsets of the regional species pool independently of any ecological process. In fact, density seems to be a good predictor of the probability of species' presence in forest fragments (e.g. Bolger et al. 1991; Tellería and Santos 1997, 1999). Additionally, species that tolerate a relatively wide range of ecological conditions are in turn more widespread and are able to occupy a large variety of habitats (Swihart et al. 2003; Bohning-Gaese et al. 2006; Hurlbert and White 2007; Carrascal et al. 2008). Therefore, pine plantations within a matrix of arable land would not selectively filter species according to the habitat characteristics of the plantations, but they would be occupied by those eurytopic species that are highly spread and abundant in the region.

However, pine plantations could impose a selective filter to the colonization by the species of the regional pool according to their strict habitat selection and spatial niches (e.g. preferences for pine foliage or trunks for foraging or nesting). The habitat requirements of bird species that are characteristic of the dominant agricultural environments, or of Mediterranean habitats with marked preferences for broadleaf sclerophyllous foliage or for a well developed understory (e.g. Tellería et al. 1999), contrast with structural characteristics provided by coniferous plantations with a generally poor shrub layer. Therefore, the habitat-matching hypothesis predicts that habitat structure of afforestations would constrain its colonization by the regional pool of species, favouring only those birds which exhibit a marked preference for coniferous trees and a high cover of the tree canopy (Santos et al. 2006; Sirami et al. 2008a, 2008b; Rey Benayas et al. 2010). Moreover, birds may have a higher colonization success of pine plantations, in a landscape dominated by arable lands, if they are able to survive in human-altered novel habitats such as urban environments. Several studies have shown that urban-exploiter birds have larger brains than urban-avoider species (Maklakov et al. 2011), probably because large-brained animals are behaviourally innovative species that have higher success and experience lower mortality when exposed to a novel environment (Sol et al. 2005a, 2007, 2008).

Some autoecological traits of bird species, such as sedentariness, body mass and clutch size may also predict the colonization success of pine plantations within the matrix of arable lands. Smaller birds usually attain high local and regional densities according to the inverse allometric relationship 'body mass–population density' (Carrascal and Tellería 1991; Gaston and Blackburn 2000), a pattern more pronounced in assemblages exploiting foliage or in habitats with a high foliage volume, in which smaller bird species predominate because of ecomorphological constraints (low body mass for hovering and hanging; e.g., Tellería and Carrascal 1994). Moreover, small body size is a predictor of establishment success across species (Cassey 2001) and is inversely related to extinction susceptibility in birds (Gaston & Blackburn, 1995; Owens & Bennett, 2000). Species that are sedentary and have large clutch sizes are more likely to occupy pine plantations, as these species are more likely to visit and explore the ecological opportunities provided by afforestation on a year-round basis and may attain high rates of population growth (Galván and Rey Benayas 2011), whereas resident species tend to rely more on innovative feeding behaviours in winter when food is harder to find (Sol et al. 2005b). In short, the factors that affect the success of pine plantations as a restoration strategy in Mediterranean croplands, as reflected by the capacity to hold bird species, can be divided into passive processes and active filters related to habitat requirements and preferences and autoecological traits of the bird species.

Here we evaluate interspecific differences in bird species occurrence in the novel fragmented habitat provided by small and young pine plantations of Central Spain, established over a predominantly treeless landscape dominated by herbaceous or woody cultures, where large mature forests of holm oak *Quercus rotundifolia* that may serve as sources of woodland bird species are very scarce. This habitat consists of an archipelago of young and small afforestations that punctuates the agricultural landscape, because it has been favoured by the EU CAP in the early 90s, and the size of the cropped fields is usually small (< 5 ha) due to the pattern of land ownership. The woodland avifauna of this region is impoverished and is dominated by species of Mediterranean origin and woodland generalists, as abundance of many forest birds decreases along a north-west/mesic to south-east/xeric gradient (Tellería and Santos 1993, 1994), especially for those of European biogeographic origin (Carrascal and Díaz 2003). The “natural experiment” associated with these plantations allows us to ascertain the relative influence of regional distribution patterns versus habitat preferences and some auto-ecological traits of the bird species in determining the occupancy of the referred novel afforested habitat. We hypothesize that bird species with a higher occurrence in afforested fields will be those with (i) broader geographical distribution, larger habitat breadth and increasing population trends in the recent years, (ii) marked preferences for woodland habitats and with high occupancy of novel habitats, and (iii) sedentary migration strategy, large clutch size and small body mass.

Materials and methods

Study area

Field work was conducted in tree plantations located in Campo de Montiel (38º 45’ 36” N, 3º 23’ 7” W; La Mancha, situated in the southern Spanish plateau; Fig. 1). The study area spreads on 440 km^2 and altitude ranges between 690 and 793 m a.s.l. The area is included within the Mesomediterranean bioclimate region of the Iberian Peninsula (Rivas Martínez 1981). The climate is continental Mediterranean with dry and hot summers and cold winters. Mean annual temperature and total annual precipitation in the area during the last 30 years were 13.7 °C and 390 mm, respectively (Agencia Española de Meteorología 2012). These figures were 16.6 °C and 359.9 mm in 2011, when bird surveys took place.

The area is a representative mosaic of different crops and semi-natural or introduced woody vegetation patches that are characteristic of large extensions of Mediterranean landscapes. Croplands were mostly occupied by herbaceous crops (wheat and barley), harvested once a year in June, and permanent woody crops (olive trees — 3 to 5 m high, and vineyards — 1 m high). Natural vegetation typically consisted of dense Holm Oak *Quercus rotundifolia* L. woodland and riparian forests that have been mostly extirpated from this region. Until 1992, woodland cover was restricted to open Holm Oak woodlands, usually grazed by sheep and goats. However, as in many other Mediterranean landscapes, the agricultural land is subjected to intensive management (e.g., irrigation of vineyards and olive groves) and land use change. A major result of land use change is the abandonment of herbaceous cropland and vineyard extirpation and their afforestation with the native Aleppo pine *Pinus halepensis* alone or mixed with holm oak or *Retama sphaerocarpa*, which has increased forest land in the last 20 years. The relative extent of major land use types according to our ortophoto analysis (taken from SigPac Geographic Information System of Farming Land, http://www.magrama.gob.es/es/agricultura/temas/sistema-de-informacion-geografica-de-parcelas-agricolas-sigpac-/, in 1-km radius circles around the center of the 31 tree plantations studied here, 97.4 km^2 in total) were the following: olive grove (18.1% of the total land area), vineyard (22.3%), dry herbaceous cropland (19.7%), and scrubland (10.2%). We identified ten additional land use types, namely, waste lands, roads and rural tracks, vineyard with olive trees, woodland, urban areas and scattered buildings, fruit groves, pasture land, pastures with scattered trees, streams, rivers and lagoons, and dried-fruit orchards, each representing between 0.3 and 7.1% of the total area. Particularly, tree plantations and woodland spread on 3.1% and 0.8%, respectively, of the above mentioned 1-km radius circles (Table 1). A previous study found that 85% of the ortophoto identification coincided with field observations of checking points (Moreno-Mateos et al. 2011).

Bird censuses

First, all pine plantations in the study area were located using both ortophotos (see source above) and Google Earth®, and were later verified in the field. We found 100 pine plantations that took place in 1992 or later. Next, we selected the plantations to be surveyed for birds, considering those with pines taller than 3.5 m and area larger than 1 ha (31 plantations; Fig. 1), which were 12-18 years old. Details on habitat structure of the 31 study pine plantations are shown in Table 1.

To asses bird occurrence in the novel habitat defined by the archipelago of pine plantations, bird censuses were carried out in spring (April and May) 2011. We did not intend to exhaustively census all the area covered by each single studied plantation because our goal was not to characterize species richness, but to establish a protocol to quantify species occurrence in the investigated novel habitat (for details on spatial variation of bird species richness with area of pine plantations in the study region, see Díaz et al. 1996 and Santos et al. 2006). Thus, only one census plot was established in each one of the 31 pine plantations, in order to avoid pseudoreplication when quantifying relative abundance of bird species in this novel habitat. We assessed the occurrence of bird species in these census plots using point-count stations (Bibby et al. 2000) lasting 10 minutes. All auditory and visual contacts were recorded, but only those within a 50 m radius (0.78 ha) were used in subsequent analyses, in order to increase the detection probability of studied species. Every census plot was surveyed twice on different days, once in the morning between sunrise and three hours later and once in the evening two hours before sunset. All censuses were conducted by the same well trained field ornithologist (JSSO) on windless (wind speed < 3 m s^{-1}) and rainless days. Nocturnal birds, aerial feeders such as swallows or swifts and raptors were not considered in data analyses, as this census method does not accurately estimate the occurrence of these species. A species was considered to be present in the census plot if it was detected in at least one of the censuses. The cumulative census time of 20 min in the two censuses carried out in each plot defines a long time devoted to bird census per unit of area, maximizes the detection probability of species and, thus, the accurate estimations of their occurrence in the habitat provided by the studied plantations (Shiu and Lee 2003).

Regional patterns of bird distribution

Three data sources were used to characterize the patterns of distribution, habitat preferences and population trends of common birds in the region around the study area. First, the distribution area of each species 150 km around the geographical centre of the study area was obtained from the National Breeding Bird Atlas (Martí and del Moral 2003) as the proportion of occupied 10 x 10 UTM km squares (308 UTM squares in total). The region defined by this circle includes the study area where Díaz et al. (1996) carried out the analysis of bird occupation of mature pine plantations during the breeding season (ca. 85 km to northeast).

Secondly, habitat breadth of the bird species in 15 main habitat categories as well as their relative abundance in woodlands, agricultural areas and urban environments within the Mesomediterranean region of Central Spain were obtained from Carrascal and Palomino (2008; electronic Appendix: http://avesbiodiv.mncn.csic.es/19mono-suppl.pdf). Habitat breadth was calculated using Levins' (1968) index, divided by the number of habitat categories considered. This index ranges between 1 (evenly distributed across the 15 habitats) and 1/15 (only present in one habitat). Relative abundances for each species were calculated by dividing the measured densities provided by Carrascal and Palomino

(2008) in each habitat by the maximum regional density recorded in the 15 main habitats of the Mesomediterranean region of Central Spain (considering the maximum density measured in three types of forests –pine, holm oak and deciduous woodlands–, five types of agricultural habitats –dry arable lands, irrigated lands, vineyards, olive groves and agricultural mosaics with woody cultivations–, and two types of urban habitats –towns and periurban developments with scattered buildings); relative abundances range between 1 (maximum density attained at that habitat) and 0 (absent). Preference of bird species for mature pine plantations in the study region was obtained from Díaz et al. (1996), and was estimated as the proportion of occupied plantations (n=48).

And third, the Spanish SACRE programme (monitoring of common breeding birds in Spain) was used to quantify the population changes of the studied species from 1998 to 2011 in Central Spain (SEO/Birdlife, 2012). Population changes were measured as the percentage of change in 2011 respect to the 1998 baseline data (see Online Resource 1).

Morphological and life-history traits of birds

Data on body mass was obtained from Cramp (1998), and information on clutch size from Lislevand et al. (2007). The migratory strategies of birds (trans-Saharan migrant, score 0 vs. resident species not migrating outside the Iberian Peninsula, score 1) in the study area were taken from Díaz et al. (1996) and Tellería et al. (1999); see Online Resource 1 for details.

Data analyses

The number of occupied afforested plots by each bird species was used as a measure of their occurrence in the novel habitat defined by the archipelago of pine plantations. The interspecific variation in occurrence was analyzed using a generalized linear model with negative binomial errors and the log-link function (Crawley 1993). In this kind of model, the response variable represents a count of the occurrence and must have only non-negative integer values, and the conditional variance of the count is given by $\mu(1+\alpha)$, where μ denotes the conditional mean and α is calculated by the model using the maximum-likelihood (ML) estimation. Statistical significance of the predictor variables (see below) was estimated using a robust approach where quasi-ML standard errors are calculated using a "sandwich" of the inverse of the Hessian and the Outer Product of the Gradient (Lindsey 2004; Cottrell and Lucchetti 2011). The negative binomial generalized linear model is a good solution for zero-inflated Poisson models where the over-dispersion parameter φ is highly deviated from one. In fact, the Poisson regression model produced a higher AIC figure (231.5) and a poorer residual plot than the negative binomial model (AIC = 183.4). Standardized regression coefficients (β) were obtained in the regression analysis (i.e., analysis was performed with standardized variables, so that their averages were zero and variances were 1). Statistical analyses were carried out using Gretl package 1.9.5cvs (http://gretl.sourceforge.net/).

It is commonly acknowledged that species are evolutionarily related throughout a phylogenetic scheme, and therefore they should not be treated as independent sample units in comparative analyses (Harvey and Purvis 1991; but see Westoby et al. 1995; Price 1997). Nevertheless, we are not interested in patterns of biological diversification throughout evolutionary time in this particular study, but only in present-day relationships pertaining to the occurrence of species in an intensively human-transformed environment. Thus, we simplified the data analyses by avoiding the complexity and drawbacks of comparative methods (i.e., uncertainty about models of evolutionary change, phylogeny topology or branch lengths).

Results

Twenty-four out of 80 terrestrial bird species of the study region were observed in the 31 tree plantations that were studied. The most widespread species were the wood pigeon *Columba palumbus* and the goldfinch *Carduelis carduelis*, which occurred in more than 80% of the pine plantations. The magpie *Pica pica* and the great tit *Parus major* were also relatively frequent, occurring in more than one-third of the pine plantations. The remaining species were relatively scarce, and 12 species were present in less than one-tenth of the plantations (Online Resource 1). Many species with marked habitat preferences for woodland habitats were very scarce (except the great tit) or were never recorded in the pine plantations (e.g. firecrest *Regulus ignicapilla*, short-toed treecreeper *Certhia brachydactyla*, long-tailed tit *Aegithalos caudatus*, nuthatch *Sitta europaea*, crested tit *Lophophanes cristatus*, great spotted woodpecker *Dendrocopos major* and European jay *Garrulus glandarius*).

Occurrence of species in pine plantations was significantly explained by a model including the ten predictor variables (χ^2_{10} = 62.34, P < 0.001; Nagelkerke pseudo R^2 = 0.640), and was significantly and positively associated with the proportion of occupied 10 x 10 UTM km squares around the study area, habitat breadth, the population trend of species within the period 1998-2011, and the occupation index of mature pine plantations in the study region (Table 2 and Fig. 2). The extent of regional distribution and habitat breadth were the two predictor variables with the highest magnitude effects according to the standardized regression coefficients. The remaining predictor variables were not significantly related to the occurrence of species in the pine plantations (P > 0.24; Table 2).

Discussion

This study clearly shows that woodland restoration based on small, highly fragmented, pine plantations in a Mediterranean landscape matrix dominated by agricultural habitats does not contribute to enhancing avian diversity by capturing woodland birds, especially if the natural forests of the region do not belong to the coniferous vegetation domain. Under these circumstances, the chance of encountering a particular species in pine plantations is the consequence of the pattern of regional distribution, instead of ecological processes mediated by preferences for a particular subset of habitats or life history traits, where the most widespread species with broader habitat preferences (eurytopic taxa) and increasing population trends are favoured.

The low influence of autoecological traits of species in determining the probability of occurrence in pine plantations is reinforced by two additional characteristics of the studied region and plantations: the low maturity and small size of pine plantations, and the low favourability of the region for the forest avifauna considering biogeographic constraints (Tellería and Santos 1993; Carrascal and Díaz 2003). The young and small isolated pine plantations, within a matrix of deforested agricultural landscape (<1% of broadleaf dry sclerophyllous forests in our study area), reduce their attractiveness for woodland specialist species, considering the fragmentation of populations as several studies have shown (e.g. Diaz et al. 1998; Izhaki 1999; Santos et al. 2002, 2006, for the Mediterranean region). Moreover, and as Shochat et al. (2001) have shown with pine plantations in Israel, pine plantations in Mediterranean zones are generally too simplistic in structure to maintain rich bird communities, mainly due to the lack of suitable microhabitats in the understory (see also López and Moro 1997). On the other hand, the studied plantations are located in a region with impoverished forest avifauna dominated by species of Mediterranean origin with marked preferences for sclerophyllous shrublands or open woodlands (Monkkonen 1994; Tellería and Santos 1994; Carrascal and Díaz 2003).

Moreover, the future aging effect for newly established plantations seems to be of minor importance favouring avian biodiversity in these plantations, because forest specialists of Mediterranean coniferous forests require larger woodland patches (Díaz et al. 1998; Santos et al. 2006). In fact, coniferous forest specialists, such as the firecrest *Regulus ignicapillus*, the crested tit *Lophophanes cristatus*, the coal tit *Periparus ater*, the nuthatch *Sitta europaea* or the crossbill *Loxia curvirostra* were very scarce or never recorded in the region, thus emphasizing the low favourability of the study area for forest avifauna of the coniferous domain. Santos et al. (2006) have also demonstrated that large mature pine plantations ($\geq$ 100 ha) in the southern plateau of the Iberian Peninsula reach an average of 16 bird species with only 3 forest specialist species, a figure considerably lower than the average of 27 species recorded in similarly mature and large pine plantations in the northern plateau (and 6 forest specialists). This observed pattern reinforces the importance of the biogeographic context when designing restoration plans based on afforestations in agricultural landscapes (Suárez-Seoane et al. 2002).

The pattern of bird species occurrence in the mosaic of pine plantations surrounded by cropland arose just as a consequence of probabilistic reasons related to the abundance and population trends of the species at a regional scale: those species occupying greater proportions of territory around the study area, exhibiting larger habitat breadth and with increasing population trends were those most frequently encountered in the plantation plots. Thus, the commonness of bird species in the study region determine their occupation of pine plantations, a result that agrees with the rather common positive relationship between regional abundance and distribution of species in many animal groups (Gaston 1994). The tight relationship between regional habitat breadth and occupancy of this novel, highly fragmented habitat, is consistent with the value of niche-based characteristics of species in explaining patterns of bird distribution from the level of local habitats to that of geographical ranges (see also, Swihart et al. 2003; Böhning-Gaese et al. 2006; Hurlbert and White 2007; Carrascal et al. 2008; Slatyer et al. 2013).

By contrast, bird species that were expected to occur most frequently in the pine plantations due to their preferences for woodland habitats and avoidance of agricultural and urban habitats (Santos et al. 2006; Sirami et al. 2008a, 2008b; Rey Benayas et al. 2010) did not exhibit a higher frequency than species with other habitat preferences. Only the occupancy of mature pine afforestations in the same region had a relevant influence on the frequency of occurrence of birds in the small and highly fragmented plantations of agricultural areas of Central Spain, although its magnitude effect was relatively low according to its standardized regression coefficient (see Table 2). Similarly, species that were expected to be good colonizers of novel habitats because of characteristics like sedentariness, large clutch size and small body size (Galván and Rey Benayas 2011), did not occur more frequently in the studied plantations than species with other autoecological traits. Therefore, our analyses indicate that the occurrence of birds in pine plantations in abandoned Mediterranean cropland is explained by the regional pattern of bird distribution, but it is poorly related to the habitat preferences and autoecological traits of the bird species. This pattern is probably the consequence of the small area of the pine plantations in the study region, determined by the scheme of land tenure of small agricultural properties. In fact, the small area of plantations, with an average of 4.6 ha and ranging between 1 and 22 ha, is considerably lower than the minimum area requirements of many woodland specialists in Central Spain that need more than 10 ha to be present, such as the stock dove *Columba oenas*, the great spotted woodpecker *Dendrocopos major*, the orphean warbler *Sylvia hortensis*, the golden oriole *Oriolus oriolus*, the Eurasian jay *Garrulus glandarius* or the cirl bunting *Emberiza cirlus* (Díaz et al. 1998).

However, it would not be correct to design restoration strategies based on pine plantations ignoring the autoecological traits of the bird species just because they cannot predict bird occurrence. Some autoecological traits of birds, in particular migratory strategy, egg mass and body mass, have been shown to predict the density, not occurrence, of bird species in other pine plantations on an agricultural matrix located in a nearby study region (Galván and Rey Benayas 2011). Bird species density in pine plantations were determined by ecological processes as expected by the fact that species that are sedentary and have small egg and body masses are good colonizers of novel habitats (Cassey 2001; Duncan et al. 2003; Galván and Rey Benayas 2011). It may thus be possible that two different indicators of the success of pine plantations in gathering bird populations, namely species occurrence and local density, are determined by different processes, the former being dependent on regional distribution at larger scales and the latter responding to the autoecological traits of species. This suggestion, however, must be taken with caution because the afforested fields of the present study are considerably smaller (mean area = 4.6 ha) than those in which bird density was found to be associated with autoecological traits of the species (area > 25 ha; Galván and Rey Benayas 2011), so processes controlling their colonization by birds cannot be straightforward compared. Future studies should investigate if bird occurrence and density are actually dependent on different factors in Mediterranean cropland afforestations.

In conclusion, pine plantations favoured by the European CAP resulting in an archipelago of man-made woodland islands within a Mediterranean agricultural landscape, only capture widespread and habitat generalist avian species with increasing population trends, not contributing to favouring truly woodland species. This result casts doubts on the value of this restoration practice for the conservation and management of avian diversity in the Mediterranean region if it is developed in very small woodland areas considering the pattern of land tenure of small properties.

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Table 1 Mean, standard deviation (sd) and range (min / max) of the habitat structure variables in 31 tree plantations and landscape cover variables around such plantations in Campo de Montiel (La Mancha, Central Spain) during spring 2011.

	mean	sd	range	
Habitat structure				
Area (ha)	4.6	3.7	1.3	21.9
Tree layer cover (%)	50.6	24.1	15.3	100.0
Average tree height (m)	4.7	1.0	3.5	7.2
Density of trunks 10-20 cm dbh (# in 0.2 ha)	79.5	42.2	16.0	168.0
Density of trunks >20 cm dbh (# in 0.2 ha)	2.7	5.7	0.0	26.0
Cover of shrubs (%)	2.8	7.2	0.0	31.7
Average shrub height (m)	0.9	1.0	0.0	2.9
Cover of the herbaceous layer (%)	46.1	39.2	0.0	100.0
Landscape cover around plantations (%)				
Streams. rivers and lagoons	0.8	1.3	0.0	4.3
Roads and rural tracks	7.1	5.2	0.2	22.1
Woodlands	3.9	4.1	0.4	18.9
Holm oak Woodland	0.8	1.5	0.0	7.4
Pine plantations	3.1	2.6	0.4	11.5
Fruit groves	1.1	1.3	0.0	5.3
Waste lands	7.1	4.2	0.0	13.3
Olive groves	18.1	21.8	0.0	68.9
Pastures with scattered trees	0.3	0.4	0.0	2.0
Scrubland	10.2	7.3	0.0	28.4
Pastures	1.3	1.6	0.0	7.7
Dry herbaceous cropland	19.7	8.8	0.0	37.7
Vineyards	22.3	14.2	0.0	45.4
Vineyards with olive trees	5.4	9.6	0.0	33.6
Dried fruit orchards	0.8	2.3	0.0	9.5
Urban areas and scattered buildings	1.8	1.9	0.0	6.7

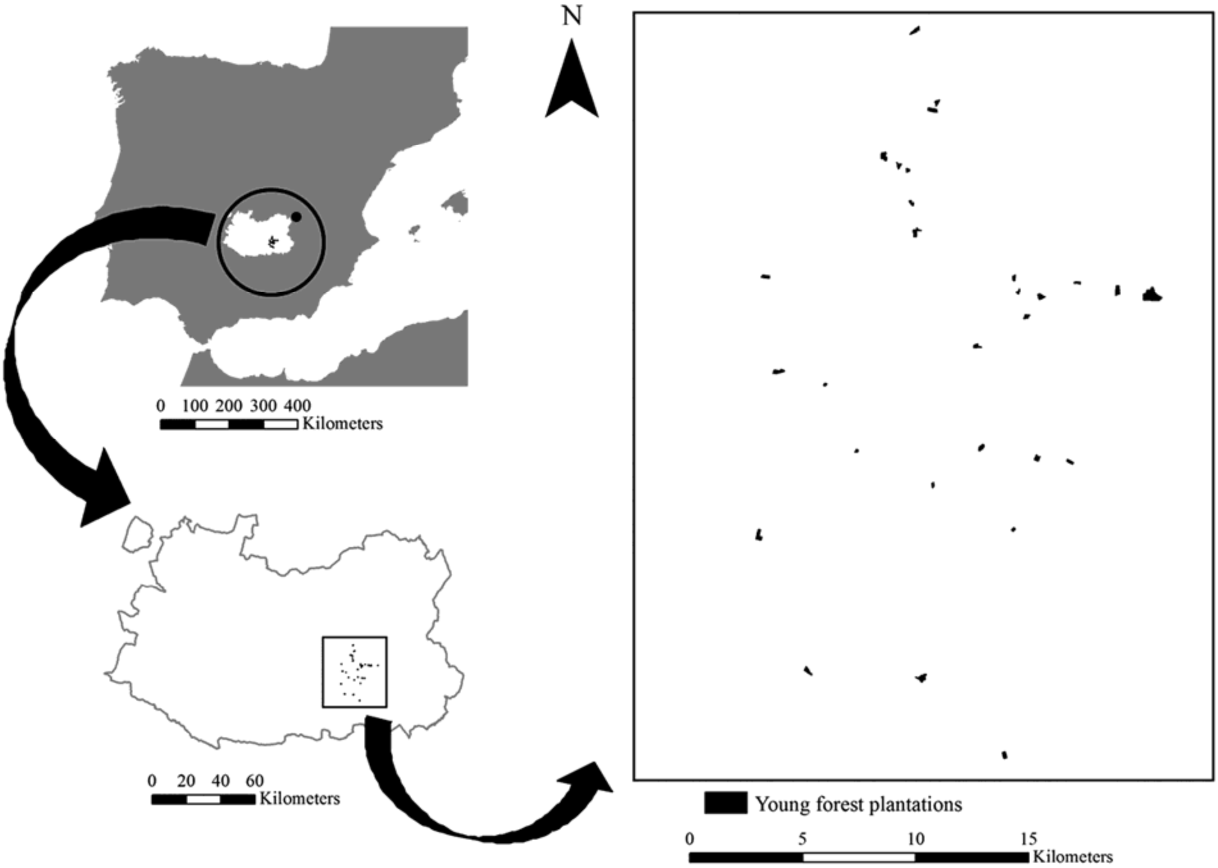
Table 2 Generalized linear regression model (with negative binomial errors and the log-link function) relating the habitat occupancy of 80 bird species in young and small pine plantations of agricultural areas of Central Spain and ten predictor variables describing regional distribution, habitat breadth, population trends (1998-2011), regional habitat preferences (four variables), migratory strategy, body mass, and clutch size. p: Statistical significances were estimated using a robust approach with quasi-ML standard errors. Regional distribution: proportion of occupied 10 x 10 UTM km squares 150 km around the study area. Occupation index of mature plantations: proportion of occupied plantations in southern xeric Iberian plateau obtained from Díaz et al. (1996). Migratory strategy: 1 - resident. 0 - trans-Saharan migrant. Coefficient: standardized regression coefficients that inform about the magnitude and sign of the partial relationships of the predictor variables and the response variable. The meaning of the rest of the variables is described in the Methods section; data for the 80 studied species can be found in Online Resource 1.

	Coefficient	se	p
Regional distribution	1.03	0.53	0.050
Habitat breadth	0.94	0.36	0.009
Population trend (1998-2011)	0.39	0.12	<0.001
Occupation index of mature plantations	0.25	0.10	0.009
Relative abundance in woodlands	-0.08	0.31	0.806
Relative abundance in agricultural habitats	-0.07	0.23	0.751
Relative abundance in urban environments	-0.03	0.22	0.903
Migratory strategy	0.29	0.24	0.236
Body mass (in ln)	-0.02	0.16	0.879
Clutch size	0.06	0.18	0.714

Legends to figures:

Fig. 1 Location of the study area (rectangle) within the Ciudad Real province (white area) in central Spain and distribution of the 31 tree plantations that were investigated in this study. A circle of radius = 150 km is centered at the baricenter of the study area, and has been used to select the UTM squares of 10x10 km^2 that have been considered to quantify the regional distribution area of each species (number of occupied UTM squares). The black dot on the gray map of the Iberian Peninsula shows the location of the study area of Díaz et al. (1996).

Fig. 2 Relationship between interspecific variation in habitat occupancy of young and small pine plantations of agricultural areas of Central Spain and regional distribution (proportion of occupied 10x10 UTM km squares 150 km around the study area), population trends (percentage of change from 1998 to 2011), regional habitat breadth, and occupation index of mature plantations (proportion of occupied plantations in southern xeric Iberian plateau obtained from Díaz et al. 1996). Habitat occupancy is the number of occupied census plots where the species were present, divided by the total number of censused plots. Sample size is 80 bird species.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Kilometers
0 20 40 60
Kilometers
Young forest plantations
0 5 10 15
Kilometers

Fig. 1

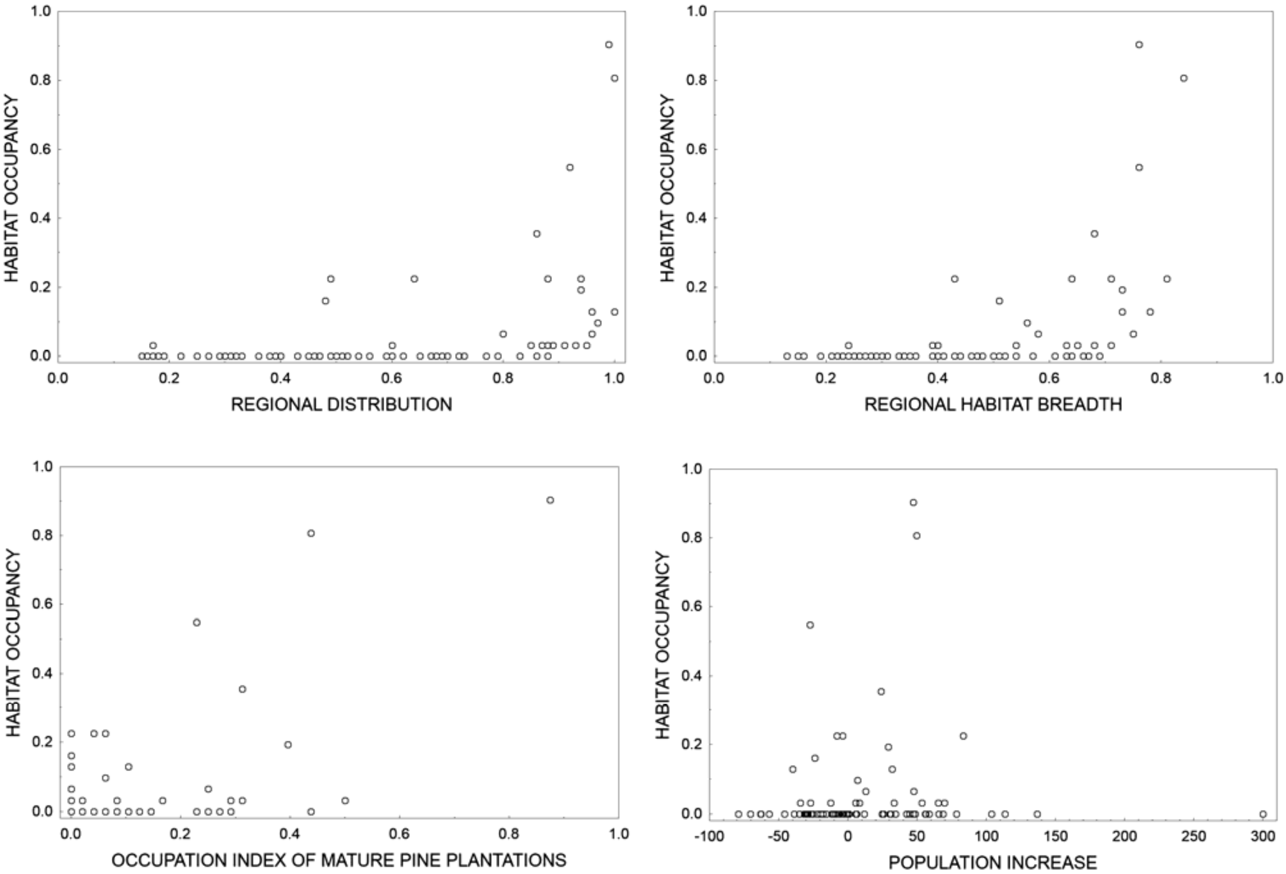
HABITAT OCCUPANCY
REGIONAL DISTRIBUTION
HABITAT OCCUPANCY
REGIONAL HABITAT BREADTH
HABITAT OCCUPANCY
OCCUPATION INDEX OF MATURE PINE PLANTATIONS
HABITAT OCCUPANCY
POPULATION INCREASE

Fig. 2