

Exotic tree plantations and avian conservation in northern Iberia: a view from a nest–box monitoring study

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Abstract

Exotic tree plantations and avian conservation in northern Iberia: a view from a nest–box monitoring study.— The spread of exotic tree plantations on the North Atlantic coast of the Iberian peninsula raises concern regarding the conservation of avian biodiversity as current trends suggest this region might become a monoculture of Australian Eucalyptus species. To shed more light on the factors promoting differences in avian communities between and within exotic tree (Monterey Pine *Pinus radiata* and *Eucalyptus* spp.) plantations and native forests in the Urdaibai area (northern Spain), this study aimed to explore (1) how the type of habitat and vegetation characteristics affect bird species richness and the settlement of some particular species during the breeding period, (2) if some reproductive parameters (*i.e.* egg–laying date and clutch size) vary among habitats in a generalist bird species (the Great Tit *Parus major*), and (3) the existence of differences among habitats in the abundance of a key food resource on which some insectivorous birds are expected to rely upon for breeding (*i.e.* caterpillars). Our results confirmed that Eucalyptus stands house the poorest bird communities, and identified understory development as an important determinant for the establishment of titmice species. Furthermore, we found that exotic trees showed lower caterpillar abundance than native Oak trees (*Quercus robur*), which might contribute to explain observed differences among habitats in bird abundance and richness in this region. However, we did not find differences among habitats in egg–laying date and clutch size for the Great Tit, suggesting that the potential costs of breeding in exotic tree plantations would occur in later stages of the reproductive period (*e.g.* number of nestlings fledged), a circumstance that will require further research.

Key word: Bird diversity, Planted forests, Land–use changes, Linear mixed models, MAB Biosphere reserve, Iberian peninsula.

Resumen

Plantaciones de árboles exóticos y conservación de la avifauna en el norte de la península ibérica: perspectiva de un estudio de seguimiento de cajas nido.— La expansión de plantaciones de árboles exóticos en la costa cantábrica de la península ibérica suscita preocupación por la conservación de la biodiversidad de aves, puesto que las tendencias actuales sugieren que esta región podría convertirse en un monocultivo de especies de eucalipto australiano. Para arrojar más luz sobre los factores que promueven las diferencias en las comunidades de aves entre y dentro de las plantaciones de árboles exóticos (pino de Monterrey *Pinus radiata* y *Eucalyptus* spp.) y los bosques nativos de la zona de Urdaibai (norte de España), el objetivo del presente estudio consistió en analizar (1) la forma en que el tipo de hábitat y las características de la vegetación afectan a la riqueza de especies de aves y el asentamiento de determinadas especies durante el período de cría; (2) si algunos parámetros reproductivos (*p.ej.* la fecha o el tamaño de puesta) varían entre los hábitats en una especie de ave generalista (el carbonero común, *Parus major*); y (3) la existencia de diferencias entre hábitats por lo que hace a la abundancia de una fuente clave de alimento de la que se prevé que las aves insectívoras dependan para la cría (las orugas). Nuestros resultados confirmaron que las poblaciones de eucalipto albergan las comunidades más pobres de aves y establecieron el desarrollo del sotobosque como un factor importante para el establecimiento de las especies de páridos. Asimismo, hallamos que los árboles exóticos presentaban una abundancia de orugas menor que la de los robles nativos (*Quercus robur*), lo que podría contribuir a explicar las diferencias observadas entre los hábitats en cuanto a la abundancia y la riqueza de aves de esta región. No obstante, no se hallaron diferencias entre los hábitats por lo que concierne a la fecha y el tamaño de puesta para el carbonero común, lo que sugiere que los posibles costes de criar en plantaciones de árboles exóticos se producirían en etapas posteriores del periodo reproductivo (*p.ej.* el número de pollos emplumados), una circunstancia que habrá que seguir investigando.

Palabras clave: Diversidad de aves, Bosques plantados, Cambio del uso de la tierra, Modelos lineales mixtos, Reserva de la biosfera del MAB, Península ibérica.

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Introduction

Increasing human demands for wood and its by-products (e.g. paper) in contemporary time (Ajani, 2011), and greater concern over the loss of natural forests, particularly in tropical regions (Gibson et al., 2011), have favoured commercial forest plantations as a main source of timber supply (Barlow et al., 2007; Brockerhoff et al., 2008). As a consequence of their profitability, forest plantations are replacing other land uses of declining economic yield (such as pastures and agricultural lands; Sohngen et al., 1999). This shift in land use is dramatically changing the socio-economic context and the landscape of many regions, with potential effects on biodiversity worldwide (Foley et al., 2005; Bremer & Farley, 2010; Felton et al., 2010). Planted forests now cover more than 264 million hectares around the world (i.e. 7% of the global forest area), and they are expanding at a rate of five million hectares per year (FAO, 2010). In spite of the growing generalization of this land use, we still have a limited understanding of the consequences of plantations on biodiversity and other ecosystem services (Louzada et al., 2010). Such circumstances restrict our ability to design sustainable management policies to preserve native flora and fauna and improve habitat quality in these exploited areas (Hartley, 2002; Brockerhoff et al., 2008).

The spread of stands of the non-native Monterey Pine (*Pinus radiata*, of North-American origin) and Eucalyptus species (mainly *Eucalyptus globulus*, native of Australia and Tasmania) have transformed the landscape of the Atlantic coast of Northern Iberia, where the original view just a century ago showed a mosaic of farmlands interspersed with hedges and coppices of natural vegetation (Lautensach, 1964). In recent decades, exotic tree plantations have progressively replaced pastures and farmlands (most of them devoted to hay production) that constitute a declining traditional activity (GV, 2005; Santos et al., in press). From the description of the bird communities of the different habitats present in Northern Iberia, several studies have raised concern about the proliferation of plantations, since they house fewer, and more generalist bird species than farmlands and natural forests (Bongiorno, 1982; Tellería & Galarza, 1990; Proença et al., 2010). Such circumstances suggest that the above-mentioned landscape modifications are impoverishing regional avifauna and probably the communities of other taxonomic groups (Proença et al., 2010; Calvino-Cancela et al., 2012). This situation may be aggravated even more as a consequence of the current drop in the prices of pine wood, since many foresters now prefer Eucalyptus plantations, which are by far the poorest habitat with regard to avian communities (Pina, 1989; Tellería & Galarza, 1990).

Observed differences among habitats in avian richness suggest that exotic tree plantations could set limits to the local distribution of some bird species. Understanding the mechanisms responsible for these patterns could help us to design recommendations to increase biodiversity in plantations (Hartley, 2002). For this purpose, it is necessary to explore how variation in some important characteristics of plantations, which are

susceptible to be managed (e.g. vegetation structure), can affect avian communities, an issue that has barely been tackled in this region. At a more detailed scale, another issue that remains to be addressed is to know how generalist bird species perform in commercial plantations and are able to persist in these habitats. The study of the ecology of these widely-distributed species, and the comparison among habitats of some relevant parameters (e.g. breeding performance, body condition) might help to understand the observed variation in their abundance, as well as the potential causes that are constraining the occurrence in plantations of other more ecologically-demanding species (Carrascal & Tellería, 1990; Tellería & Galarza, 1990; Proença et al., 2010).

In this study, we explored how habitat type and vegetation structure can affect species richness and the settlement of birds during reproduction in a study site located in northern Spain. We performed bird counts and monitored nest-boxes in seven localities representing the three main forest habitats of the area (natural Oak forests, and Pine and Eucalyptus plantations). We also analysed how some breeding parameters (egg-laying date and clutch size) varied in the Great Tit *Parus major*, a generalist species occurring at lower densities in plantations (Tellería & Galarza, 1990). Given that breeding success in the Great Tit and other species may depend on particular food resources (i.e. defoliating caterpillars; Visser et al., 2006; Wilkin et al., 2009), we also estimated caterpillar abundance, which is expected to differ between natural forests and exotic tree plantations, because a number of native phytophagous arthropods might be unable to thrive in the latter (Kolb, 1996). With this approach, our goal was to go one step forward in this research topic and shed additional light on the mechanistic factors that might be promoting variation in bird abundance and composition in plantations and natural forests in Northern Iberia.

Methods

Study area and nest-box study design

Fieldwork was carried out in the UNESCO-MAB Biosphere Reserve of Urdaibai (Bizkaia province, Basque Country, Spain) and some surrounding municipalities (i.e. Bakio, Ereño and Ea). The study site is located within the North Atlantic coast of Iberia, an area where it is possible to find farmlands, Pine and Eucalyptus plantations, and a few remnants of natural Oak *Quercus robur* forest. This latter formation constitutes the climax forest ecosystem that would develop in many of the areas currently occupied by farmlands and exotic trees (Loidi et al., 2009).

During mid-February 2012, we installed 212 nest-boxes in seven localities. These localities were not randomly selected but were previously identified as large enough to house at least 20 nest-boxes. Large patches of forest are rare in this region, which is characterized by the presence of a complex mosaic of small private plots that are normally devoted to

different land-uses. Selected localities represented the three main wooded habitats of the region: three plots of Eucalyptus plantations in Jata (denoted as Euc-1 in the figures; 43° 24.855' N, 02° 51.778' W), Ea (Euc-2; 43° 22.063' N, 02° 35.649' W) and Mañu (Euc-3; 43° 24.744' N, 02° 47.041' W); three plots of Pine plantations in Arteaga (Pinus-1; 43° 21.595' N, 02° 39.633' W), Ereño (Pinus-2; 43° 20.739' N, 02° 36.783' W) and Matxitxako (Pinus-3; 43° 26.434' N, 02° 44.888' W); and one Oak forest in Arratzu (Oak; 43° 17.767' N, 02° 38.236' W), the only forest in the area that was large enough to hold a reasonable number of nest-boxes. Within each locality, nest-boxes were hung from a nail hammered into the tree trunk at about 3.5 m height and separated approximately 50 m from each other. However, we finally considered a reduced subset of nest-boxes ($n = 186$), because 26 disappeared during the course of the study, with between 18 and 42 nest-boxes remaining per site (see fig. 2A). Nest-boxes were checked regularly (at least once per week) from early April to late June to determine the laying date of the first egg (assuming a production of one egg per day) and clutch size of the nest-boxes occupied by birds. Although we were particularly interested in obtaining measurements of chicks' body condition, we failed in this purpose because anomalous bad weather conditions in May caused the death of recently hatched chicks or, less frequently, clutch desertion. In the end, only 32 chicks from eight Great Tit broods were able to fledge (from two to six fledglings per brood).

Bird counts, vegetation structure and estimation of caterpillar abundance

In mid-May, we also established 10 bird count stations in each of the seven localities. Each bird count station surveyed the proximity of a previously installed nest-box, all randomly selected from all the nest-boxes available within each locality. Surveys at bird count stations lasted five minutes and we annotated all the bird species that were detected (heard or seen) within a 25-m radius. All counts were conducted in the morning (between dawn and 11:00 h) and on non-rainy days without strong winds that could affect the reliability of our sampling protocol.

Variation in the structure of avian communities and bird reproductive performance among wooded formations are likely to be the result of variation in vegetation structure among habitats. With the purpose of separating effects of habitat and vegetation structure, we also characterized the vegetation around each nest-box (25 m of radio) using nine variables: (1) general cover of shrubs (%), (2) cover of deciduous shrubs (%), (3) average shrub height (m), (4) tree cover in the canopy (%), (5) deciduous tree cover (%), (6) average tree height (m), (7) number of tree stems with a diameter higher than 40 cm, (8) average tree trunk diameter (cm), and (9) number of tree and shrub species. Given that some of these variables were expected to be strongly correlated with each other, we performed a principal component analysis (PCA) to obtain a smaller number of uncorrelated variables

(the principal components, PCs), which were easier to interpret. For this purpose, we used the program STATISTICA 7.0 and a varimax rotation of factors. Such PCA yielded three independent components (table 1). PC1 values were associated with the age of the trees, PC2 was positively correlated with variables indicating a more developed shrub layer, and PC3 represented an index of tree cover development in the canopy (see factor loadings in table 1).

As stated above, each tree species may hold a different invertebrate community, a circumstance that could affect avian richness and breeding performance (Kolb, 1996; Hartley et al., 2010). We used specific sampling methods to roughly estimate among-habitat relative abundance of the favourite invertebrate prey item used by some insectivorous birds (particularly by the Great Tit) to feed their chicks (*i.e.* caterpillars, order Lepidoptera; Visser et al., 2006; Wilkin et al., 2009). For this purpose, we placed one plastic washbasin (diameter of 42 cm) on the ground, near the trunk of 23 trees (seven Oaks, eight Eucalyptus and eight Pines). Washbasins were partly filled with water and were also covered with a metallic mesh to avoid other animals (*e.g.* large mammals) having access to the water and affecting our caterpillar estimates. This method allowed us to collect drowned caterpillars which had descended from the canopy to the ground for pupation (see Zandt, 1994). Washbasins were checked approximately once per week between mid-April and late June, and the overall accumulated number of caterpillars found in each washbasin was used as a response variable in the statistical analyses.

Statistical analyses

First, we used linear mixed models (LMM) to explore the existence of differences between habitats in vegetation characteristics (PCs). Next, we used generalized linear mixed models (GLMMs) with Poisson errors to analyze whether bird species richness obtained from count stations varied among habitats, after controlling for vegetation characteristics (Zuur et al., 2009). A similar approach to the latter, but with a binomial error distribution, was performed to test habitat and vegetation effects on the probability of nest-boxes to be occupied (binary variable; empty nest-box = 0, occupied nest-box = 1). For the 25 first clutches detected for the Great Tit (see Results), we also tested for differences between habitats in egg-laying date (*i.e.* LMM) and clutch size (*i.e.* GLMM with Poisson errors). All these models were fitted in R using the package *lme4* (Bates & Maechler, 2010). A Markov-Chain-Monte-Carlo sampling procedure (1×10^4 iterations) implemented in the package *languageR* was used to obtain the *P*-values for the fixed effects in the models analysing vegetation characteristics and egg-laying dates (Baayen, 2008). All previous analyses included locality as a random factor. Furthermore, we explored whether the number of collected caterpillars per washbasin differed among tree species. For this purpose, we performed a Kruskal-Wallis test.

Results

Variation in vegetation structure among habitats

Tree size or age (PC1) varied among habitats, with the Oak forest showing intermediate values of PC1 that did not differ significantly from the scores recorded in Pine (estimate = -1.148 ± 0.923 , $t [n = 99] = -1.25$, $P = 0.216$) or Eucalyptus plantations (estimate = 0.601 ± 0.809 , $t [n = 117] = 0.74$, $P = 0.458$), but PC1 was significantly higher in Pine than in Eucalyptus stands (estimate = 1.75 ± 0.572 , $t [n = 156] = 3.06$, $P = 0.003$). Eucalyptus plantations did not differ significantly in shrub development (PC2) from the values recorded in Pine plantations (estimate = 0.064 ± 0.39 , $t [n = 156] = 0.17$, $P = 0.869$). However, our Oak forest had a more developed understory than both types of exotic tree plantations, although this effect was only significant for the comparison with Pine plantations (Oak–Pine comparison: estimate = 0.845 ± 0.26 , $t [n = 99] = 3.26$, $P = 0.002$; Oak–Eucalyptus comparison: estimate = 0.909 ± 0.545 , $t [n = 117] = 1.67$, $P = 0.097$). For PC3, Pine and Eucalyptus plantations showed similar values (estimate = 0.021 ± 0.218 , $t [n = 156] = 0.1$, $P = 0.923$), these being significantly lower than those observed in the Oak forest (Oak–Pine comparison: estimate = 2.124 ± 0.15 , $t [n = 99] = 14.18$, $P < 0.001$; Oak–Eucalyptus comparison: estimate = 2.146 ± 0.303 , $t [n = 117] = 7.09$, $P < 0.001$).

Bird species richness

We recorded a total of 18 species (all passerines) after performing the 70 bird count station surveys (data are available from the authors upon request). Variation in bird species richness was better explained by habitat effects (see fig. 1) than by variation in vegetation structure (PC1 effect: estimate \pm SE = 0.119 ± 0.109 , $Z [n = 70] = 1.09$, $P = 0.275$; PC2 effect: estimate \pm SE = 0.147 ± 0.084 , $Z [n = 70] = 1.75$, $P = 0.081$; PC3 effect: estimate \pm SE = -0.033 ± 0.135 , $Z [n = 70] = -0.25$, $P = 0.807$). Thus, Eucalyptus plantations were the poorest habitat and differed significantly in species richness when compared to Pine plantations (estimate = 0.773 ± 0.269 , $Z [n = 60] = 2.87$, $P = 0.004$) or the Oak forest (estimate = 1.205 ± 0.422 , $Z [n = 40] = 2.86$, $P = 0.004$). Pine plantations and the Oak forest showed similar values of species richness (estimate \pm SE = 0.27 ± 0.505 , $Z [n = 40] = 0.534$, $P = 0.593$; fig. 1).

Nest–box occupancy rates

Out of the 186 nest–boxes considered in the study, 43 were occupied by birds for reproduction. We considered occupied nest–boxes as those in which eggs were laid. The Great Tit was the most common breeding species ($n = 31$) and the only species occurring in the seven localities (fig. 2A). Less frequently, we detected Coal Tits *Periparus ater* ($n = 6$) and Blue Tits *Cyanistes caeruleus* ($n = 6$). We arbitrarily distinguished between Great Tits' first and second clutches taking advantage of the fact that Coal Tits and Blue Tits are single–brooded

Table 1. Correlation coefficients (factor loadings) between the nine variables characterizing vegetation structure (VS) and the three principal components derived from the PCA. Eigenvalues and the percentage of variance explained by each component are also shown: 1. Overall shrub cover (in %); 2. Deciduous shrub cover (in %); 3. Average shrub height (in m); 4. Tree cover (in %); 5. Deciduous tree cover (in %); 6. Average tree height (in m); 7. Number of tree stems ($d > 40$ cm); 8. Average tree trunk diameter (in cm); 9. Number of tree and shrub species.

Tabla 1. Coeficientes de correlación (cargas factoriales) entre las nueve variables que caracterizan la estructura de la vegetación (VS) y los tres componentes principales derivados del análisis de componentes principales (ACP). También se muestran las raíces latentes y el porcentaje de la varianza explicados por cada componente: 1. Cubierta arbustiva total (en %); 2. Cubierta de arbustos caducifolios (en %); 3. Altura media de los arbustos (en m); 4. Cubierta arbórea (en %); 5. Cubierta de árboles caducifolios (en %); 6. Altura media de los árboles (en m); 7. Número de árboles ($d > 40$ cm); 8. Diámetro medio del tronco de los árboles (en cm); 9. Número de especies arbóreas y arbustivas.

VS	PC1	PC2	PC3
1	-0.22	0.80	0.27
2	-0.05	0.87	0.01
3	0.50	0.61	0.32
4	0.39	-0.11	0.76
5	-0.09	0.27	0.85
6	0.89	-0.01	0.10
7	0.88	-0.09	-0.06
8	0.93	0.08	0.17
9	0.11	0.80	-0.06
Eigenvalue	2.93	2.50	1.52
Explained variance	0.33	0.28	0.17

species (see appendix 1 for more details). Second clutches were only observed in six cases (their laying dates ranging from day 55 to day 68), all of them occurring in nest–boxes installed in Eucalyptus stands (fig. 2A), but they were not statistically more frequent in these plantations (results not shown). The overall percentage of occupied nest–boxes varied greatly among localities (ranging from four 4 to 40%; see fig. 2A). In our statistical model, shrub development (PC2) was the only significant factor affecting the probability of a nest–box to be occupied (PC2 effect: estimate = 0.493 ± 0.213 ,

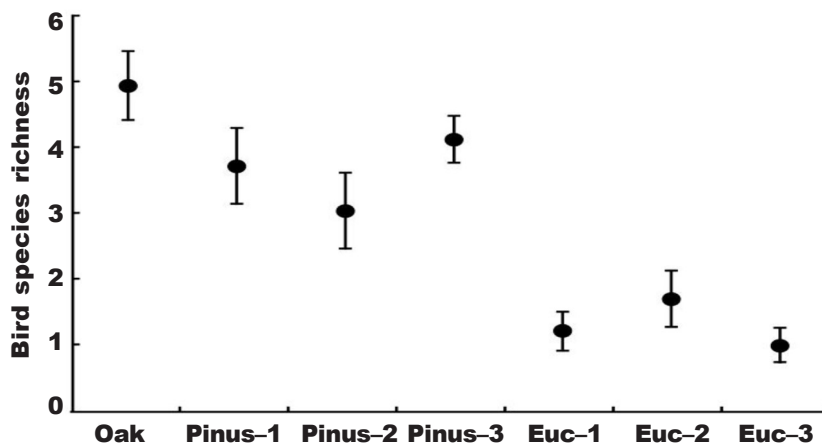


Fig. 1. Variation among localities in the number of bird species detected (*i.e.* species richness; mean \pm SE) during five minute bird counts at stations (10 random bird counts per locality).

Fig. 1. Variación entre localidades en el número de especies de aves detectadas (riqueza de especies; media \pm EE) durante recuentos de cinco minutos en las estaciones (10 recuentos aleatorios de aves por localidad).

$Z [n = 186] = 2.32, P = 0.021$; fig. 2B), while habitat type (post-hoc analysis Pine vs. Eucalyptus: estimate = $0.472 \pm 0.67, Z [n = 156] = 0.71, P = 0.481$; post-hoc analysis Oak vs. Eucalyptus: estimate = $1.421 \pm 0.858, Z [n = 117] = 1.66, P = .098$), PC1 (estimate = $-0.163 \pm 0.312, Z [n = 186] = -0.52, P = 0.602$) and PC3 (estimate = $-0.151 \pm 0.312, Z [n = 186] = -0.48, P = 0.629$) did not show significant effects.

Egg-laying date and clutch size in the Great Tit

For the 25 first clutches identified for the Great Tit, egg-laying date did not differ among Eucalyptus (mean date = 18 [18th of April] ± 5.3 d, $n = 8$), Pine (mean date = 24 [24th of April] ± 5 d, $n = 9$) and Oak stands (mean date = 21 [21st April] ± 5.3 d, $n = 8$; habitat effects: $P > 0.05$), but clutches were laid later in nest-boxes presenting older trees in their surroundings (PC1 effect: estimate = $10.17 \pm 4.16, t [n = 25] = 2.45, P = 0.024$).

Great Tit clutch size ranged between five and eight eggs. Clutch size was not affected by habitat (post-hoc analysis Pine vs. Eucalyptus: estimate = $-0.01 \pm 0.212, Z [n = 17] = -0.05, P = 0.964$; post-hoc analysis Oak vs. Eucalyptus: estimate = $-0.108 \pm 0.393, Z [n = 16] = -0.27, P = 0.784$), or by vegetation structure effects (PC1, PC2 and PC3 effects: $P > 0.05$).

Caterpillar abundance among habitats

The total number of caterpillars collected per wash-basin differed among habitats (Kruskal-Wallis test: $H_{2,13} = 10.4, P = 0.006$; fig. 3), with washbasins located under Oak trees containing a higher accumulated number of caterpillars than both Pine and Eucalyptus trees, where caterpillars were nearly absent.

Discussion

Our study confirms that the bird communities of Eucalyptus stands are significantly impoverished, with species richness during the breeding period being lower in commercial plantations than in natural forests. We also identified understory development as a main factor affecting the nest-box occupancy rate of titmice species in the study area. Thus, a more developed shrub layer increased the chances of a nest-box being occupied for breeding. Likewise, a significant difference in caterpillar abundance was observed between exotic and native trees. Although observed variation among habitats in this food resource might affect some reproductive parameters in bird species relying upon caterpillars for breeding, we did not detect differences in the breeding performance of Great Tits during the earliest stages of their reproductive process (*i.e.* egg-laying date and clutch size).

There is increasing concern about the burgeoning proliferation of exotic tree plantations around the world (Brockhoff et al., 2008; Bremer & Farley, 2010; Putz & Redford, 2010), a trend that is also expected to have a pervasive impact in many areas of the Iberian Peninsula (Santos et al., 2006; Veiras & Soto, 2011). In coastal areas of northern Spain, the transformation of traditional land-uses (*i.e.* farmlands and pastures) into tree plantations seems to be an inexorable process that might imply the decline of many open-habitat bird species that normally would not occur in woodlands. Paradoxically, these open-habitat species were originally favoured by ancient human deforestation and farming (Tellería & Galarza, 1990; Williams, 2006). In order to maintain current regional avian biodiversity, conservation efforts should be channelled into pre-

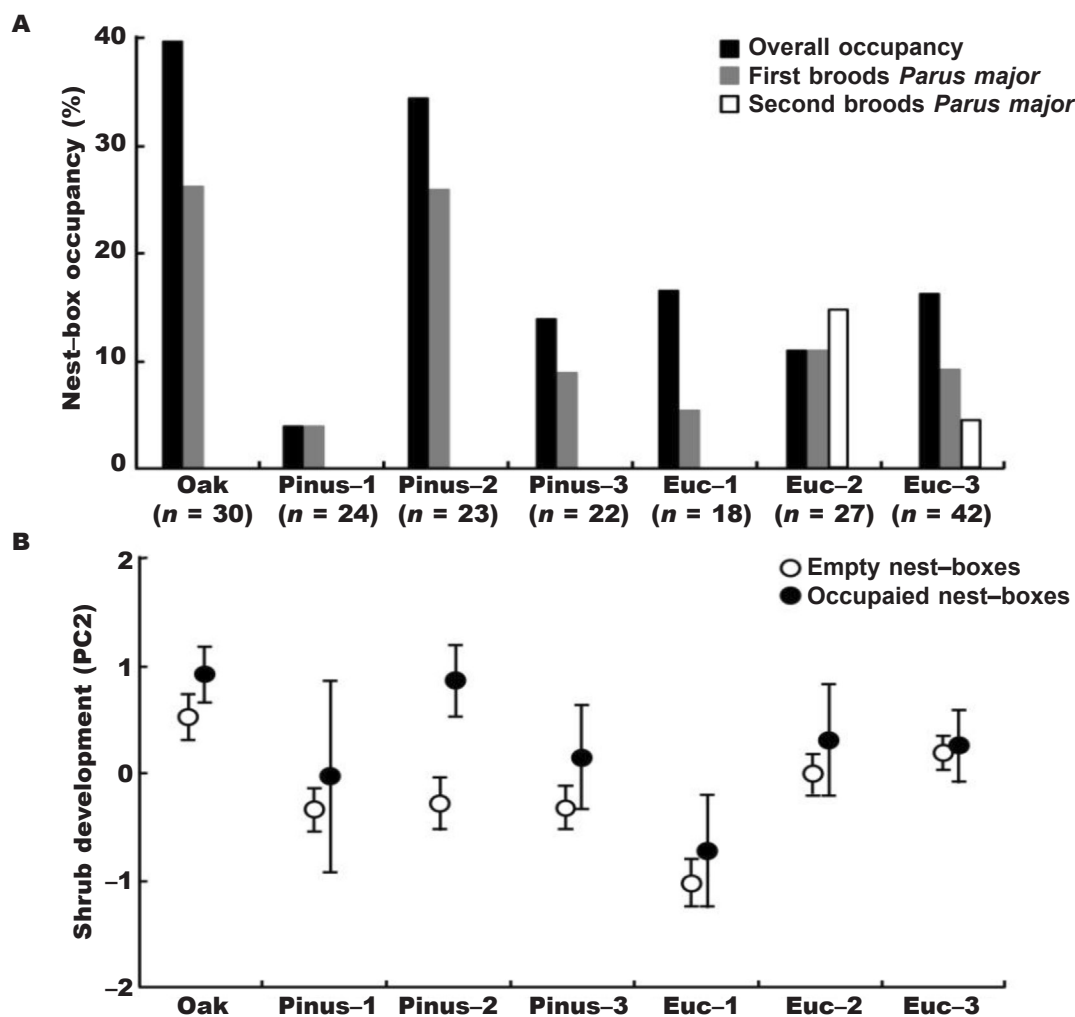


Fig. 2. A. Variation in the overall percentage of nest-boxes occupied by birds (black bars), and the percentage of Great Tit first (grey bars) and second clutches (open bars) among localities. Occupied nest-boxes were those in which eggs were laid. The number of available nest-boxes per locality is shown below the abscissa axis. B. Differences in understory development (mean \pm SE of PC2) between empty and occupied nest-boxes for the seven study sites.

Fig. 2. A. Variación en el porcentaje total de las cajas nido ocupadas por aves (barras negras) y el porcentaje de primeras (barras grises) y segundas (barras blancas) puestas del carbonero común entre localidades. Las cajas nido ocupadas eran aquellas en las que se habían puesto huevos. El número de cajas nido disponibles por localidad se muestra a continuación en el eje de las abscisas. B. Diferencias en el desarrollo del sotobosque (media \pm EE de PC2) entre las cajas nido vacías y ocupadas de los siete lugares del estudio.

servicing conventional farmlands, which hold a singular avian breeding community and are also an important wintering destination of many European migratory populations (Tellería et al., 2008; Santos et al., in press). On the other hand, the generalization of tree plantations can be considered an opportunity to recover the woodland species that had been confined to the remnants of natural forest scattered throughout this region (Quine & Humphrey, 2010; Navarro & Pereira,

2012). However, our results confirm that exotic tree plantations are not able to fulfil the role of natural forests (Bongiorno, 1982; Tellería & Galarza, 1990; Proença et al., 2010) because they lack some bird species with high demands for old forest stands, such as the European Nuthatch *Sitta europaea* (only present in the Oak forest) and the Short-toed Treecreeper *Certhia brachydactyla* (common in American Pine formations but completely absent from Eucalyptus stands).

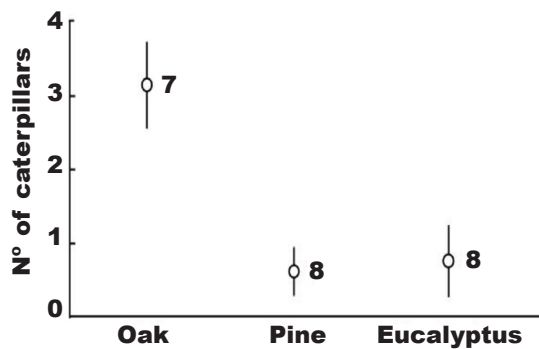


Fig. 3. Variation among Oak, Pine and Eucalyptus trees in the overall number of caterpillars collected. Graph shows means with standard errors and sample sizes.

Fig. 3. Variación entre el roble, el pino y el eucalipto en cuanto al número total de orugas recogidas. En el gráfico se muestran las medias con los errores estándar y los tamaños muestrales.

The previously-described scenario raises the need to develop management practices that help commercial plantations diversify their bird communities. A conventional solution to achieve this purpose would consist of promoting a well-developed natural shrub layer (López & Moro, 1997; Santos et al., 2006). This measure should be weighed in relation to wildfire risk, but it could be feasible in our study area given that plantations have a less complex understory than natural forests. This is probably a consequence of the regular removal of native scrublands in exotic tree stands (Veiras & Soto, 2011), which would be depicted in the lower values of PC2 in exotic tree plantations compared to the Oak forest. However, our results showed no clear association between understory development and bird richness obtained from bird counts ($P = 0.081$; see Results). We did detect, nevertheless, that shrub development may benefit the settlement of some hole-nesting sedentary species (*i.e.* Titmice species) known to attract other breeding (migratory) species that use year-round residents as cues for habitat selection (Forsman et al., 2009). At this point, we should point out that we provided birds with nest-boxes in all the study localities. Consequently, promoting a complex understory might be ineffective if nesting holes are a prerequisite for the settlement of birds during reproduction, because most exotic tree stands have very few natural cavities. This is particularly true for Eucalyptus plantations in the Basque Country, where trees are logged at a relatively early age (normally after 11 years of tree growth; Veiras & Soto, 2011), explaining the difficulty of finding Eucalyptus stands with high scores of PC1 in our study area.

In many European regions, Great Tits and other insectivorous forest bird species normally try to synchronize the hatching of their eggs with a short peak of tree defoliating caterpillars, which constitute an abundant and suitable food resource for feeding their chicks (Sanz et al., 2003; Visser et al., 2006). Although we used a very rough method based on washbasins to estimate caterpillar abundance (Zandt, 1994), our approach allowed us to corroborate that caterpillars are much rarer in exotic trees (both Pine and Eucalyptus) than in native Oaks. Such circumstance might affect the reproductive performance of Great Tits (Kolb, 1996). However, egg-laying date and clutch size did not differ among habitats, and only an effect of tree size/age (PC1) on egg-laying date emerged from our analyses, a finding that was difficult to interpret.

Although our sample size was relatively small ($n = 25$) and limited to only one year, the lack of variation between habitats in egg-laying date and clutch size agrees with the results obtained by Kolb (1996), who detected that exotic trees only had a negative effect on later stages of the reproductive period. Unfortunately, owing to bad meteorological conditions, we could not collect sufficient data from Great Tit chicks to explore this possibility. Kolb's study was carried out using a more Northern European population of Great Tits, which seems to be more dependent on caterpillar availability (Kolb, 1996; Wilkin et al., 2009). Consequently, it remains to be tested whether similar patterns will be detected in our population for which caterpillar availability is actually very low according to the data obtained from the use of washbasins, and also whether this food resource in the diet of the chicks will tend to be replaced by other invertebrates (*e.g.* spiders; Pagani-Núñez et al., 2011).

In conclusion, our results further support the negative consequences of exotic tree stands for birds at community level (*i.e.* bird species richness), with these penalties being stronger in Eucalyptus than in Pine plantations. The study went one step further and explored the possibility that differences in the composition of bird species composition be explained by vegetation structure. Also we tested the existence of variation among habitats in the reproductive performance of a generalist bird species (the Great Tit) and found a marked difference between exotic and native trees in caterpillar abundance, two aspects that had not been considered before in our study area. Although limited and preliminary as a consequence of the reduced sample size and the use of only one year of data, the patterns we observed establish the basis for future research into the observed variation among habitats in bird abundance and composition in the North Atlantic coast of Iberian peninsula.

Our study also highlights the difficulty of uncoupling habitat from vegetation structure effects in the analyses, because management practices in this region (*e.g.* age at which trees are logged) differ notably depending on the exotic tree species considered (Eucalyptus vs. Pine). Together with the scarcity of Oak forests, these circumstances made it virtually impossible to find Eucalyptus, Pine and Oak stands with similar vegetation characteristics, preventing a realistic separation of the

relative contribution of effects of habitat and vegetation structure on our response variables. Clarifying this issue could therefore help us to assess whether the conservation value of planted forests in Northern Iberia is constrained by exotic trees themselves or by the management practices they undergo (Sax, 2002).

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Appendix 1. Identifying second clutches of Great Tit.

Apéndice 1. Determinación de las segundas puestas de carbonero común.

Great tits are facultative multiple breeders and some pairs can undertake a second breeding attempt. Second clutches contain fewer eggs than first clutches and may be more frequent in some habitats than in others, possibly affecting the reliability of our between-habitat comparisons. We used the laying dates of two species known to be single-brooded (i.e. Blue Tit *Cyanistes caeruleus* and Coal Tits *Periparus ater*) to show the existence of second clutches in the Great Tit. According to the range of egg-laying dates in Blue Tits and Coal Tits (i.e. from day 4 to day 39 considering the 1st of April as day 1; see fig. A), we considered that Great Tit clutches laid later after May 11th (day 41) were second clutches, and they were consequently, excluded from the statistical tests that analysed nest-box occupancy rate, laying date, and clutch size.



Fig. A. Comparison between the laying dates of Great Tits *Parus major* and the laying dates of two single-brooded species (i.e. Coal Tit *Periparus ater* and Blue Tit *Cyanistes caeruleus*). Note that there are some overlapping data points.

Fig. A. Comparación entre las fechas de puesta del carbonero común *Parus major* y las de dos especies de puesta única (carbonero garrapinos *Periparus ater* y herrerillo común *Cyanistes caeruleus*). Nótese que algunos datos se superponen.