



Original Research Article

Effects of eucalyptus plantations on avian and herb species richness and composition in North-West Spain

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ABSTRACT

Eucalyptus plantations have been established in many areas of the world due to their fast growth and profitability. In NW Spain, *Eucalyptus* plantations now cover a larger area than native forests. Although *Eucalyptus* plantations have been shown to affect biodiversity, relatively few studies have compared their effect on multiple taxonomic groups and different aspects of biodiversity. We compared herb and bird species richness and bird abundance between 14 paired patches of native deciduous forest and *Eucalyptus* plantations in a heterogeneous agro-forest region of NW Spain. We also investigated whether *Eucalyptus* plantations contribute to shifts in community composition by analysing species nestedness and turnover. We found that species richness of both herbs and birds was consistently lower in *Eucalyptus* plantations compared to native forests. Furthermore, the abundances of bird species characteristic of agricultural, forest, scrubland and other habitats, were all much lower in *Eucalyptus* plantations than in native forests. Herb and bird communities were also significantly dissimilar between the two habitats, but as a result of different ecological processes. Species turnover explained variation between habitats in herb composition, such that species present in native forests were typical for both farmland and forest habitats, whereas those present in *Eucalyptus* plantations were typical for scrub and farmland habitats. In contrast, bird assemblages showed a significant nested subset pattern, with fewer species in *Eucalyptus* plantations compared to native forests. In total, the relative abundance of cavity-nesting forest birds was at least 64% higher in native forests. Our results show that *Eucalyptus* plantations cannot replace native forests as they harbour different herb species and only a subset of the bird species found in native forests. Considering the current rate of increase of *Eucalyptus* plantations and the fragmentation of native forests in NW Spain, a lack of conservation of native forests could result in future loss of biodiversity in general and forest specialist species in particular.

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1. Introduction

During the past 60 years, increasing human demands for wood and paper have favoured the use of fast-growing tree species for plantation forestry (Brockhoff et al., 2008). An estimated 25% of the global planted forest area (264 million ha) now consists of fast-growing exotic species, while natural forests are rapidly declining and increasingly fragmented (FAO, 2010). Exotic plantations are often preferred because of their high productivity and are seen as more economically profitable than native species.

Because of their fast growth, wide adaptability and profitability for paper production (Turnbull, 1999), *Eucalyptus* species are one of the most widely used *taxa* in intensive plantations outside their natural range, currently covering c. 20 million ha in temperate, tropical and subtropical regions (Rejmánek and Richardson, 2011). *Eucalyptus globulus* Labill. is currently one of the most important planted tree species in the world, with an estimated 2.5 million ha being planted worldwide by 2004, mainly in the Iberian Peninsula (Potts et al., 2004). In Spain, *Eucalyptus* plantations cover 633,000 ha (Montero and Serrada, 2013), having their highest densities in the North-West region (IFN, 2017). In this region, plantations of both *E. globulus* and *E. nitens* have been established in scrublands and farmlands, thus replacing traditional elements of the agrarian mosaic (Loidi, 2017). Furthermore, *Eucalyptus* plantations have also replaced native forests directly (Teixido et al., 2010). These plantations have been supported by the government (Calviño-Cancela et al., 2012), aiming at economically benefitting rural livelihoods. In NW Spain, this development has been reinforced by rural abandonment. Because of low opportunity costs and management requirements, *Eucalyptus* plantations are commonly regarded as one of the few options for land owners not living in rural areas to make use of their lands, which in turn provokes a profound change in land use.

Research has shown that *Eucalyptus* plantations have a lower species diversity of plants (Barlow et al., 2007; Proença et al., 2010; Calviño-Cancela et al., 2012) and birds (Bongiorno, 1982; Pina, 1989; Tellería and Galarza, 1990; Barlow et al., 2007; Proença et al., 2010; Calviño-Cancela, 2013; De la Hera et al., 2013), compared to native forests. This difference is not only caused by plantations tending to be younger than native forests, since also *Eucalyptus* plantations older than 25 years fail to provide habitat as suitable as native forests for many plant species (Calviño-Cancela et al., 2012). However, surprisingly few studies have analysed if the replacement of native forests by exotic plantations affect rare or specialist species to a greater extent than common generalist species (Proença et al., 2010; Calviño-Cancela et al., 2012), e.g. by analysing if there are systematic patterns in community dissimilarity between native forests and *Eucalyptus* plantations (Olden et al., 2004). Changes in community dissimilarity can in turn be elucidated by analysing species nestedness and turnover (Baselga et al., 2007). Species nestedness occurs when species assemblages in sites with fewer species are subsets of species assemblages at richer sites (Ulrich and Gotelli, 2007). In contrast, spatial turnover implies a systematic replacement of some species by others, as a consequence of environmental sorting or spatial and historical constraints (Qian et al., 2005).

In this study, we analysed whether patches of native forest have a higher species richness of herbs and birds and higher abundance of birds than patches of *Eucalyptus* plantations. Higher biodiversity in native forests can be expected as a result of a long history of low-intensity land-use resulting in species-rich plant and bird communities, as well as a result of more benign habitat characteristics of native forests (Cordero Rivera, 2011). In addition, we analysed if *Eucalyptus* plantations lead to biotic homogenization driven by a systematic loss of rare or specialist species (McKinney and Lockwood, 1999), or species turnover, where different species predominantly occur in either native forests or in plantations. We focused on herbs and birds since they are commonly used as biodiversity indicators but are characterized by different mobility and degree of habitat specificity, and therefore can be expected to respond differently to local habitat characteristics (Ekroos et al., 2013).

2. Materials and methods

2.1. Study area

The study was performed in the centre of Galicia (Ulloa Shire), in the NW of the Iberian Peninsula. The study area consisted of a hilly mosaic farmland-forest mixed landscape, of 421 km² and at an altitude of between 400 and 750 m above sea level. 46% of the area is forested, both by natural forests and plantations (IGE, 2012). Native deciduous forest is largely comprised of oak (*Quercus robur*), chestnut (*Castanea sativa*) and birch (*Betula alba*), classified as Rusco aculeati – Quercetum roboris and Holco mollis – Betuletum celtiberiace forest associations (Amigo et al., 2017). However, during the past 25 years, *Eucalyptus* plantations have increased rapidly in Galicia (Manuel and Gil, 2002), and now cover an area larger than that of native forest (500,000 ha *Eucalyptus* spp. vs 400,000 ha native forests in 2016) (IFN, 2017). Most land in Galicia is privately owned, and 83% of the *Eucalyptus* plantations in the region are on private land. During the past 30 years, 70% of the agricultural land in Galicia was abandoned (IGE, 2012), paving the way for *Eucalyptus* plantations, which are normally harvested 15–18 years after plantation, in order to re-grow or re-plant them.

The plantations of *Eucalyptus* species in the study region have mainly replaced natural and semi-natural habitats that would have been mostly covered by native forests by natural succession if left unmanaged (Calviño-Cancela et al., 2012). *Eucalyptus* plantations have also directly replaced native forest, even though this is restricted by law (DOG, 1989; Calviño-Cancela et al., 2012). Thus, although native forests still remain, particularly in mountainous areas, *Eucalyptus* plantations have increasingly contributed to the fragmentation of native oak forests (Teixido et al., 2010). Because *Eucalyptus* plantations are replacing land with high potential for natural regeneration into native forests (Calviño-Cancela et al., 2012), if left

undisturbed by management or abiotic factors (such as fire), a comparison of biodiversity between these plantations and native forests can inform about how *Eucalyptus* plantations affect future biodiversity (Stephens and Wagner, 2007).

We performed a comparative study based on 14 pairs of matched patches of native forest and *Eucalyptus* plantation (Appendix A). Patches within each pair were matched on size (≤ 12 ha size difference, mean \pm SD = 5.6 ± 3.4 ha) and patches within pairs were situated ≤ 15 km apart, mean \pm SD = 7.4 ± 3.3 km). All patches were surrounded by farmland, scrubland or a mix of these two. All of the *Eucalyptus* plantations were of intermediate age (between 8 and 15 years old; cf. Calviño-Cancela et al., 2012). Of the 14 *Eucalyptus* plantations studied, only two were pure stands. The remaining plantations had other marginal tree species (mainly oak), comprising 0.33–25% of the trees, that grew scattered between the *Eucalyptus* trees (Appendix B). Only four out of 14 *Eucalyptus* plantations were actively managed, mainly by removal of undergrowth each year. The four managed plantations had less than 50% cover of shrubs (mainly *Erica*, *Ulex* and *Cytisus* species), while shrub cover in the remaining plantations ranged between 50 and 80% (see Appendix B for information about patch vegetation characteristics). There was no significant difference in patch sizes between patch types ($t_{26} = -0.56$, $P = 0.5802$; native forests: mean size 33.7 ha, range 11–62 ha; *Eucalyptus* patches: mean size 31.3 ha, range 10–70 ha; Appendix B).

2.2. Surveys

Data were collected between early May and late August in 2017, when two visits to each pair of patches were performed. All surveys for the 14 pairs of patches were done by the same person. Each pair of patches was surveyed on the same day (cf. Kleijn et al., 2006) and the order in which the surveys were carried out within the pair was systematically switched between visits, to avoid effects of time of day (cf. Dänhardt et al., 2010).

2.2.1. Plant surveys

In three 20×20 -m square plots within each patch, separated by 250 m along a 500 m transect across the centre of the patch, herbaceous plants (subsequently referred as herbs) species were identified (cf. Santos et al., 2010). We used the total number of plant species observed during both survey rounds to calculate species richness and composition.

2.2.2. Bird censuses

Birds were censused along 500-m long transects placed across the centre of the patch. All birds observed or heard were recorded up to a distance of 25 m on each side of the transect (Tellería and Galarza, 1990). The transect length was a compromise between maximizing survey area whilst avoiding edge effects, which could bias results because of patch size or geometry. Bird censuses were carried out over the entire breeding season (mid-April to end of August) during a 2-h period starting after sunrise. Birds observed flying over the study patches were not included in analyses due to inadequacy of the transect method to survey them (Calviño-Cancela, 2013).

2.3. Quantification of vegetation parameters and bird habitat groups

Eight different vegetation characteristics were recorded: number of trees, number of species of trees, tree diameter at breast height (DBH), tree height, percentage of canopy cover, number of species of shrubs, shrub height, and percentage of shrub cover (De la Hera et al., 2013; Appendix B). All these parameters were recorded visually and by the same observer (following Santos et al., 2010), within each of the three 20×20 m sample plots described above, except concerning number of trees and DBH which were instead measured in three sub-squares of 8×3 m within each 20×20 m plot. All values were averaged between sample plots in order to obtain a single descriptor for each vegetation characteristic for each patch. Number of trees and DBH were first averaged per sample plot and then per patch.

Since the eight vegetation parameters estimated in each study patch were inter-correlated, we used principal components analysis (PCA) to create a set of uncorrelated vegetation descriptors (De la Hera et al., 2013). From the eight original vegetation variables introduced in the PCA, we selected the three first principal components (PCs), which together explained 73.1% of the total variation (Table 1). Our main goal was to characterize the two patch types, rather than directly analyse effects of vegetation structure on birds and herbs. We interpreted PCs by correlating them to the original vegetation variables (function `cor.test`). PC1 was positively correlated with the number of trees in each study patch and negatively to tree species richness, canopy cover and shrub species richness (Table 1). Thus PC1 was interpreted as a measure of structural and taxonomic forest diversity. PC2 was negatively correlated with shrub height and positively with tree height and tree diameter (Table 1), characterising a gradient in tree size whereas PC3 was positively correlated with the percentage of cover of shrubs (Table 1).

To test if birds associated with different habitats were affected by *Eucalyptus* plantations to different degrees, we classified all observed bird species into four habitat groups according to how they are classified by the European Bird Census Council (EBCC, 2014): farmland, forest, scrubland and undetermined, i.e. species neither breeding in farmland nor forest (habitat category “other” in EBCC; Appendix D).

2.4. Statistical analyses

We evaluated differences in vegetation characteristics (PCs) between patch types using *t*-test. Linear mixed models (function `lme()` available in library `nlme`; Pinheiro et al. (2011)) were used to estimate the effect of patch type (native vs exotic)

Table 1

Loadings of the eight studied vegetation parameters on the three principal components (PC1, PC2 and PC3) used in the analyses and cumulative percentage of explained variance per PC. The vegetation parameters correspond to: number of trees (N_trees), tree diameter at breast height (DBH), tree height (Tree_height), number of species of trees (N_sp_trees), percentage of canopy cover (P_can_cov), number of species of shrubs (N_sp_shrub), percentage of shrub cover (P_cov_shrub) and shrub height (Shrub_height).

Vegetation parameter	PC1	PC2	PC3
N_trees	0.492		
DBH	-0.219	0.441	0.423
Tree_height		0.595	0.177
N_sp_trees	-0.454		-0.404
P_can_cov	-0.482	0.127	-0.15
N_sp_shrub	-0.46		
P_cov_shrub	-0.229	-0.233	0.744
Shrub_height		-0.601	0.219
% of explained variance	0.4301	0.6001	0.7312

on species richness of herbs and birds, and abundance of birds. Because the study was based on 14 matched pairs of native and *Eucalyptus* forest patches, we initially used pair as a random factor in analyses. However, accounting for the matched structure, it had no or only marginal effect on the results; for bird richness and abundance the random effect was estimated as zero, whereas for herbs species richness the random effect was marginally non-significant (LR = 3.18, df = 1, P = 0.07). Since all analyses of herb species richness were qualitatively the same when and when not accounting for the paired structure (not shown), we for simplicity present all results without accounting for the paired structure. In addition, although the study was not designed to investigate the effect of patch size, we checked if analyses were affected by patch size by including patch size (logged) as a covariate. However, since patch size did not relate to herb species richness, bird species richness or bird abundance (effect of patch size in model also accounting for patch type, P > 0.233 in all cases), it was not considered further. Herbs and birds species richness and bird abundance were therefore analysed in separate models with only patch type as factor. All models were assessed for normality and homoscedasticity (cf Quinn and Keough, 2002). Bird species richness was log transformed to achieve normally distributed residuals. For both bird models, we found heterogeneity of variances between patch types, with a higher residual variance in *Eucalyptus* than in native patches. We therefore adjusted the variance-covariance structure for patch type in these models using the varIdent()-function available for mixed models in nlme (Zuur et al., 2009). We also related herb species richness, bird species richness (log-transformed) and bird abundance to the PCs describing vegetation structure using linear regression (function cor.test).

We analysed species nestedness and spatial turnover of both herb and bird species using nestedness and turnover partitioning of community dissimilarity as implemented in library betapart (Baselga et al., 2012). For this approach, we calculated Sørensen's dissimilarity based on presence-absence matrices for herbs and birds, and dissimilarity matrices were used to calculate nestedness and turnover components. Nestedness and turnover in bird and herb communities was thereafter analysed using permutational analysis of variance (function adonis() implemented in library vegan; Oksanen et al. (2013), including patch type as a fixed factor (Jacoboski et al., 2016). P-values were derived based on 999 permutations (Oksanen et al., 2013). All statistical analyses were done using R 3.2.3 (R Core Team, 2008).

3. Results

3.1. Vegetation parameters

Eucalyptus plantation and native forest patches differed significantly in PC1 ($t_{26} = 14.32$, $P < 0.0001$), indicating that *Eucalyptus* plantations have a much higher density of trees, but a much lower tree and shrub species richness and canopy cover (Fig. 1A) compared to native forests. PC2 and PC3 did not significantly differ between patch types ($t_{26} \leq 0.59$, $P \geq 0.3823$), indicating that tree size and shrub development did not significantly differ between native forests and *Eucalyptus* plantations (Fig. 1B–C).

3.2. Herbs

We found a total of 31 herb species in native forest patches (6.8 ± 3.5 (mean \pm SD) per plot and 9.7 ± 2.9 per patch) and 27 herb species in *Eucalyptus* patches (4.1 ± 1.4 per plot and 7.1 ± 1.9 per patch). There were twelve species only observed in native forest patches and eight species only observed in *Eucalyptus* patches (Appendix C). In native forest patches the most frequent herbs were typical of mixed and deciduous temperate forests, whereas plants in *Eucalyptus* patches mainly belonged to scrublands or mesophilic to wet meadows and pastures (Appendix C).

Herb species richness was significantly related to patch type ($t_{26} = 2.84$, $P = 0.0087$), being higher in native forest compared to *Eucalyptus* patches (Fig. 2A). Herb species richness was associated with structural and taxonomic forest diversity (i.e. decreasing herb species richness with increasing PC1; $r_{26} = -0.44$, $P = 0.019$, Fig. 1D), but not with tree size or shrub development ($P > 0.83$ in both cases, Fig. 1E–F).

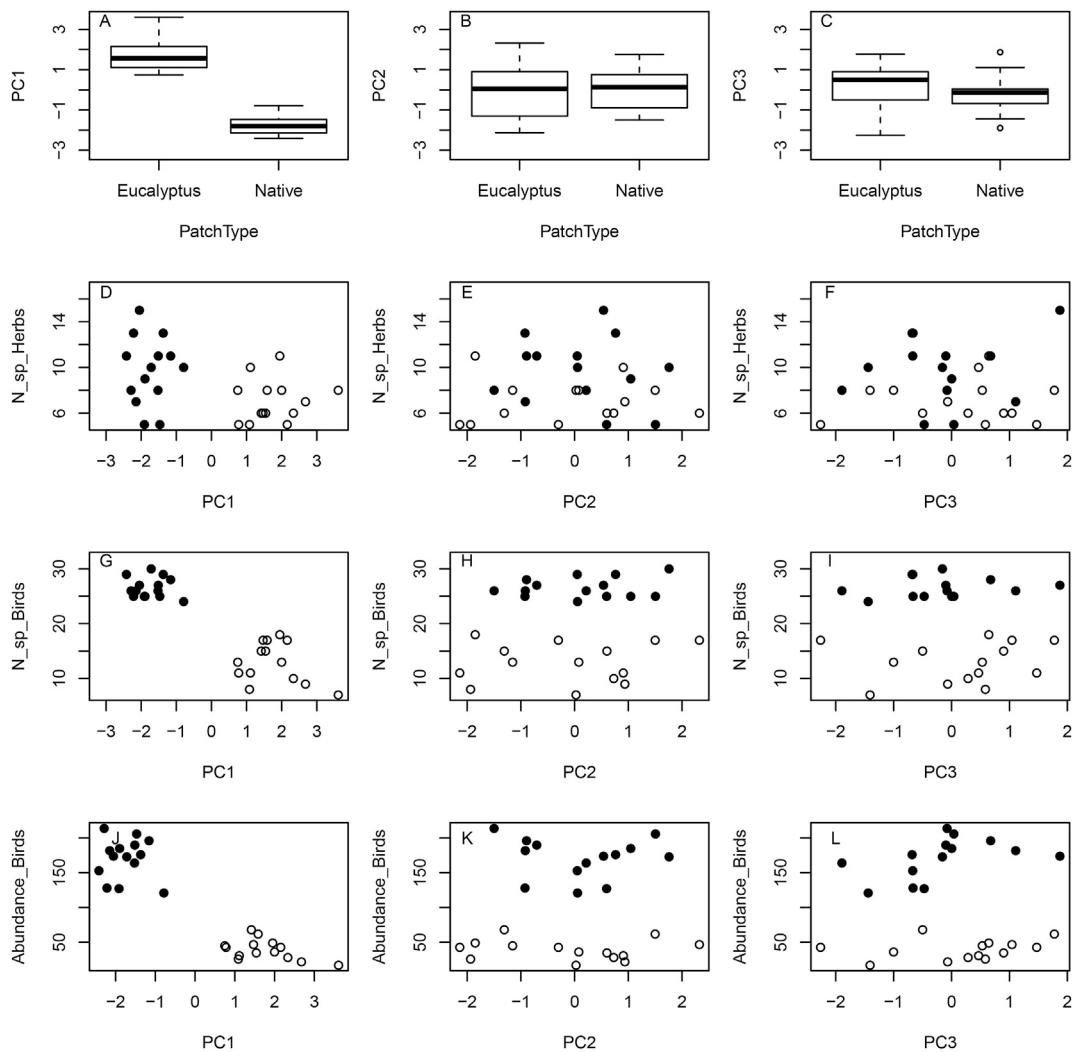


Fig. 1. Forest characteristics (PC1-PC3) for the two patch types (panels A–C) and the relationships between herb species richness (panels D–F), bird species richness (panels G–I), and bird abundance (panels J–L) on one side and forest characteristics (PC1-PC3) on the other. PC1 corresponds to patch structural and taxonomic diversity; PC2 relates to tree size and PC3 to shrub development. Filled dots correspond to native forest patches and empty dots correspond to *Eucalyptus* patches.

Herb species did not show a nestedness subset pattern between native forest and *Eucalyptus* patches ($F_{1,26} = 0.223$, pseudo- $R^2 = 0.008$, $P = 0.653$). In contrast, herb communities were significantly different from each other between native forest and *Eucalyptus* patches, based on significant turnover between patch types ($F_{1,26} = 7.623$, pseudo- $R^2 = 0.227$, $P = 0.001$).

3.3. Birds

We observed 2,384 birds belonging to 37 species in native forest patches and 548 birds of 34 species in *Eucalyptus* patches. The average number of bird species in native forest patches was 26.1 ± 1.7 and that of *Eucalyptus* patches 12.8 ± 3.7 . Four species were only observed in native forest patches (*Prunella modularis*, *Sylvia communis*, *Turdus viscivorus* and *Upupa epops*) and one species only in *Eucalyptus* patches (*Accipiter nisus*) (Appendix C).

Bird species richness was significantly higher in native forests patches than in *Eucalyptus* patches ($t_{26} = 9.29$, $P < 0.0001$; Fig. 2B). Bird species richness was significantly associated with structural and taxonomic forest diversity (PC1, $r_{26} = -0.901$, $P < 0.0001$, Fig. 1G), but not with tree size or shrub development ($P > 0.45$ in both cases, Fig. 1H–I).

Bird abundances were consistently higher in native forest patches compared with *Eucalyptus* patches, independently on the birds' habitat association ($t_{26} = 5.95$, $P < 0.0001$ for farmland birds; $t_{26} = 11.89$, $P < 0.0001$, for forest birds; $t_{26} = 7.91$, $P < 0.0001$ for scrubland birds; and $t_{26} = 7.91$, $P < 0.0001$, for birds from undetermined habitat; Fig. 3). Bird abundance was

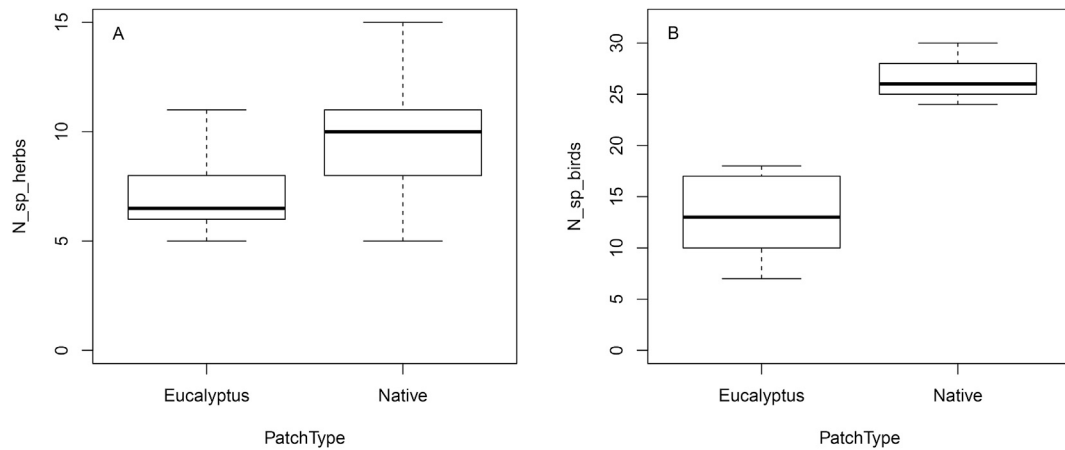


Fig. 2. Boxplots on the species richness of herbs (panel A) and birds (panel B) in *Eucalyptus* and native forest patches.

significantly associated with structural and taxonomic forest diversity (PC1, $r_{26} = -0.914$, $P < 0.0001$, Fig. 1J), but not with tree size or shrub development ($P > 0.72$ in both cases, Fig. 1K–L).

Bird communities were strongly nested in response to patch type ($F_{1,26} = 109.89$, pseudo- $R^2 = 0.82$, $P = 0.001$), with exotic plantations demonstrating a systematic overall homogenisation of bird assemblages. The analysis on bird community turnover returned a negative F-value and was therefore discarded.

4. Discussion

We found that herb and bird species richness were consistently higher in native forest patches compared to *Eucalyptus* patches, demonstrating that native forests provide much richer habitats for birds and herbs compared to *Eucalyptus* plantations. These results agree with previous studies in the North of the Iberian Peninsula, both for plants (Proença et al., 2010; Calviño-Cancela et al., 2012; Bas López et al., 2018) birds (Bongiorno, 1982; Pina, 1989; Tellería and Galarza, 1990; Proença et al., 2010; Calviño-Cancela, 2013; De la Hera et al., 2013; Bas López et al., 2018) and other taxa (Cordero-Rivera et al., 2007; Calviño-Cancela et al., 2013). In addition, we also found consistently higher abundance of birds in native forest patches compared to *Eucalyptus* patches, irrespective of the habitat characteristics of the birds. This supports our hypothesis

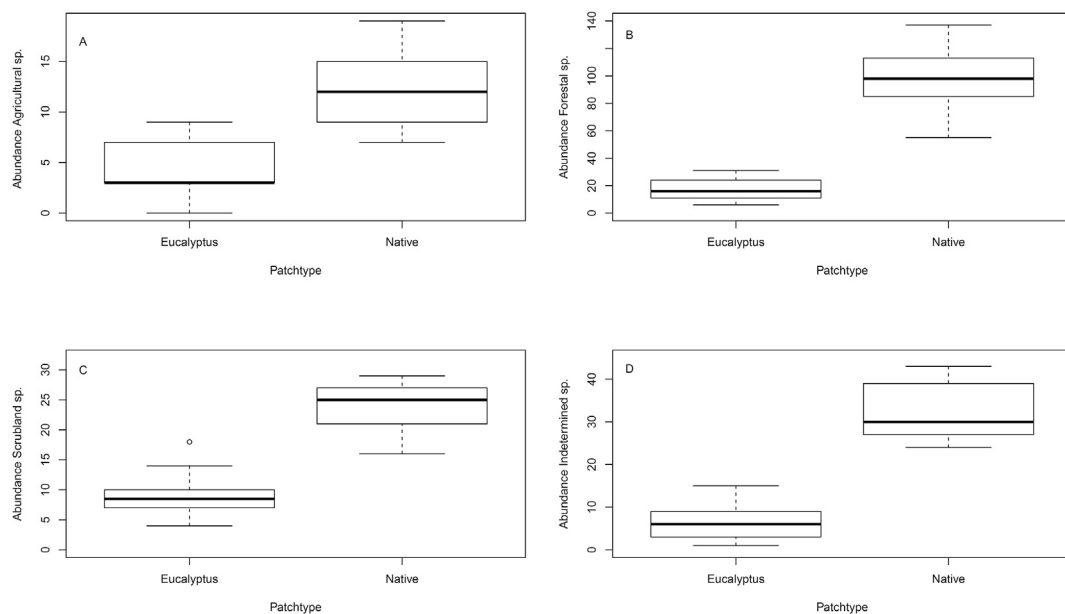


Fig. 3. Boxplots on bird abundances per transect in relation to patch type for birds with different habitat associations: Farmland species (A), Forest species (B), Scrubland species (C) and species from Undetermined habitat (D), in *Eucalyptus* and native forest patches.

that habitat quality in *Eucalyptus* plantations is inferior to that in native forests, not only for forest birds, but also for farmland, scrubland and birds from undetermined habitat. We also found that *Eucalyptus* plantations significantly contributed to community nestedness in birds, demonstrating that *Eucalyptus* plantations lead to biotic homogenization of bird communities compared to native forests (cf. Jacoboski et al., 2016). Furthermore, we found that there was a significant spatial turnover of herb species between native forests and *Eucalyptus* plantations. Thus, in addition to reducing local herb species richness, exotic plantations are also characterized by different plant species compared to native forests. Our results show that *Eucalyptus* plantations have a lower species richness of birds and herbs, and contribute to biotic homogenization in bird assemblages and spatial turnover of herb communities. Taxon-specific responses suggest that *Eucalyptus* plantations do not have resources to support diverse bird assemblages on the one hand, whereas biological legacy and prior disturbance disrupt plant communities in *Eucalyptus* plantations, on the other hand.

In our study, the main differences between native and exotic patches were the density of trees and the species richness of trees and shrubs. While the density of trees was much higher in *Eucalyptus* plantations, the species richness of trees and shrubs was much lower (cf. Bas López et al., 2018). The difference in forest structure between native forests and *Eucalyptus* plantations might to a large extent explain the differences in species richness for both birds and plants, although the exact ecological mechanisms for both taxa remain unclear. Decreasing numbers of trees, and increasing tree and shrub species richness in native forests were strongly associated with high species richness for both herbaceous plants and birds, as well as more abundant bird assemblages. Plantations in the study area are usually established including one (*Eucalyptus nitens*) or two (*E. nitens* and *Pinus radiata*) tree species which are densely planted, with some naturally occurring species, usually *Quercus robur*, being able to grow between the planted trees. In native forests *Q. robur*, *Castanea sativa* and *Betula alba* typically dominate, and thus the species richness in native patches in our study was 3.7 tree species and 11.1 shrub species on average, compared to only 1.9 and 6.9 in *Eucalyptus* plantations (Appendix B). Furthermore, mechanical and chemical (mineral fertilizers and biocides) land preparations before *Eucalyptus* plantations are carried out may also result in loss of important aspects of biodiversity. Other characteristics of plantations, not estimated in this study, such as the homogeneity in tree age, lack of dead wood and old trees may also contribute to reduced plant and bird biodiversity in *Eucalyptus* plantations (Cunningham et al., 2005). Finally, we found a lack of difference in shrub development in our study between native forests and *Eucalyptus* plantations (Fig. 1C), contrary to previous studies (De la Hera et al., 2013). In our study, only two plantations had the understory cleared every year, which is the common scenario in the area due to rural abandonment (Marey-Pérez et al., 2006). Therefore, if plantations in the study area were more regularly cleared, as may be the case in more populated areas, we would expect to find larger differences in shrub development. Nevertheless, even though shrub development was not significantly different between both patch types, shrub species richness was still higher in native forests.

Whilst both herb and bird species richness was consistently lower in plantations, we found that herb species and bird communities were affected in different ways. First, we found a significant turnover in herb species between native forests and *Eucalyptus* plantations. In native forest patches the most frequent herbs were typical of mixed and deciduous temperate forests, whereas plants in *Eucalyptus* patches mainly belonged to scrublands or mesophilic to wet meadows and pastures (Rivas-Martínez et al., 2002; Appendix C). In addition, we found eleven species of herbs only present in native forest patches, all of which are typical for managed pastures, wood fringes or deciduous forests with wet soils. In contrast, the seven herb species that were found exclusively in *Eucalyptus* patches are all typical for pastures and scrubland communities (Rivas-Martínez et al., 2002; Appendix C). Therefore, there is a turnover between native forest patches, including species with varying habitat requirements, and *Eucalyptus* plantations, mostly including species typical for meadows and scrublands (see also Proença et al., 2010). This result may be explained by a combination of biological legacy (Franklin et al., 2000) and habitat variability amongst native forests. Native forests established on abandoned farmland can harbour herb species that are typically found in pastures, due to biological legacy effects. As native forests mature, they acquire wet and shady soil conditions which mainly benefit forest specialist species. Therefore, patches of native forests in our study together contain a big range of herb species, typical for either abandoned pastures or wet forest soils, depending on forest maturity. By contrast, plantations have mostly been established in farm- and scrubland, reflecting the biological legacy of communities present in the area before the plantations were established. With time, *Eucalyptus* plantations are known to change soil conditions (Bargali et al., 1993; Souto et al., 2001; Martín et al., 2011; Lombao et al., 2015) and induce local scarcity of water (Núñez et al., 2006; Cordero Rivera, 2011; Yang et al., 2017), with detrimental effects on forest habitat specialists. Therefore, current herb communities in *Eucalyptus* plantations are the result of assemblage processes that include local legacy effects, involving species already present on the area (Ibbe et al., 2011), and species that spread from surrounding habitats after the local habitat alteration (Calviño-Cancela et al., 2012). Together, these assembly processes, in addition to the changes in soil and water conditions that affect forest species to be established in *Eucalyptus* plantations, most likely explain the dissimilarity between native forest and plantation communities. In addition, intensive management practices in *Eucalyptus* plantations during harvest may change soil properties (Rab, 1994) with potential consequences for plant communities. Hence, *Eucalyptus* plantations cannot substitute native forest habitats, as they will not support the forest herb species that typically appear in native forests (Calviño-Cancela et al., 2012).

In contrast to herbs, we found that *Eucalyptus* plantations lead to a systematic loss of bird species, consistent with biotic homogenisation. The observed nestedness in bird species was mainly driven by declines in forest species and some habitat generalists, as nine forest species and five habitat generalist species found in native forests were either absent or very infrequently observed in *Eucalyptus* patches (Appendix D). In our study we observed one species that was only present in *Eucalyptus* plantations (*Accipiter nisus*, Appendix D). This species is known to be a forest species that has adapted well to

modern tree plantations, although it is not exclusively found in them (Hesterkamp, 2015). In addition, our results showed that bird abundances were consistently higher in native forest patches compared to *Eucalyptus* patches irrespectively of habitat affiliations. Interestingly, even though we found more scrubland herb species in *Eucalyptus* plantations than in native forests, bird species typical of scrubland habitats appeared in consistently lower numbers in *Eucalyptus* plantations. This fact is probably the result of fewer species of shrubs in *Eucalyptus* plantations than native forests, which is related to a lower total bird species richness and abundance (Fig. 1G and J). In addition, this lower abundance of scrubland birds in *Eucalyptus* plantations could be also due to differences in habitat structure caused by higher tree density and lack of open spaces in these plantations as compared to native forests (Fig. 1A), impeding scrubland birds to establish in plantations. Therefore, this result suggests that, even though *Eucalyptus* plantations harbour more scrubland herb species because of biological legacy, the lower number of shrub species and the high tree density that occur in the *Eucalyptus* plantations do not provide resources needed by some scrubland bird species to use this habitat. Regarding forest species found in both patch types, 80% of the total number of forest birds seen was found in native forests (Appendix D). The strong differences in forest specialist bird assemblages can be partly explained by the presence of old trees and large trunks in native forests, providing tree holes and other nesting sites, which are not present in *Eucalyptus* plantations (Carrascal and Tellería, 1990). In our study, all primary or secondary nest cavity breeding bird species, such as *Cyanistes caeruleus*, *Dendrocopos major*, *Parus major*, *Periparus ater*, *Sitta europaea* and *Sturnus unicolor*, were all at least 79% more abundant in native forests patches, except *Picus viridis* which was 64% more abundant (Appendix D). Furthermore, the physical and chemical characteristics of *Eucalyptus* trees are known to reduce lichens and other epiphytes, as well as herbivorous insects (Cadahia, 1980; Calviño-Cancela et al., 2013), and therefore potentially bird food resources, which may contribute to the differences we found in bird diversity, especially that of insectivorous birds. Similar to herbs, the current bird communities in *Eucalyptus* plantations may be shaped by past community composition and new species arriving from surrounding landscapes after the plantation. In contrast to herbs, the high mobility of birds may reduce species turnover between native forest and *Eucalyptus* plantations. Instead, species establishment is filtered by niche availability, which is lower in *Eucalyptus* plantations, leading to nestedness and lower abundance or absence of forest specialists in *Eucalyptus* plantations.

We found a higher variance in bird species richness within the *Eucalyptus* patches studied compared to the native forest patches. This heterogeneity was likely driven by differences in management practices in the *Eucalyptus* plantations and the resulting effect on structural forest diversity (see Fig. 1A, D G and J). Our results show that more diverse *Eucalyptus* plantations are associated with higher bird species richness, but structural diversity in plantations is not allowed according to current legislation which states that tree plantations must be managed and the undergrowth cut in order to prevent fires (BOE, 2012). We therefore suggest that allowing more diverse plantations could mitigate bird biodiversity loss, by increasing nesting sites and food availability (Calviño-Cancela, 2013), although it would never replace native forest habitats and their biodiversity richness.

It has been suggested that increasing plantation age might mitigate biodiversity loss (Calviño-Cancela et al., 2012). In our study, we compared biodiversity in natural mature forests with *Eucalyptus* plantations that were predominantly young, such that we could not analyse if increasing age of *Eucalyptus* plantations could benefit birds or plants. However, this scenario reflects the real situation in the study region, since the vast majority of *Eucalyptus* plantations are harvested much before reaching maturity, i.e. 15–18 years after establishment. Furthermore, whereas allowing for longer rotations in *Eucalyptus* plantations may palliate biodiversity loss in these plantations, the dramatic differences in bird nestedness and abundance, and herb turnover suggest that this is very unlikely to compensate for native forest loss. The unsuitability of *Eucalyptus* plantations to many herb and bird species might instead decrease the connectivity between existing native forest patches and thereby increase fragmentation and dispersal barriers between local populations.

5. Conclusions

Our results showed that *Eucalyptus* plantations constitute a much poorer habitat for both plants and birds than native forests, with significantly lower species richness in both taxa, and a lower abundance of birds. In addition, because *Eucalyptus* plantations drive biotic homogenization of birds and species turnover in herbs, an increasing extent of exotic plantations at the expense of native forests would most likely lead to further biodiversity loss, with the strongest effect on forest specialists. Our results are in line with other studies, demonstrating negative effects of *Eucalyptus* plantations on other taxa (e.g. Cordero-Rivera et al., 2017), suggesting that increasing these plantations at the expense of native forest would affect biodiversity in general. Therefore, the conservation of native forest patches in the study area should be a priority if biodiversity loss is to be avoided.

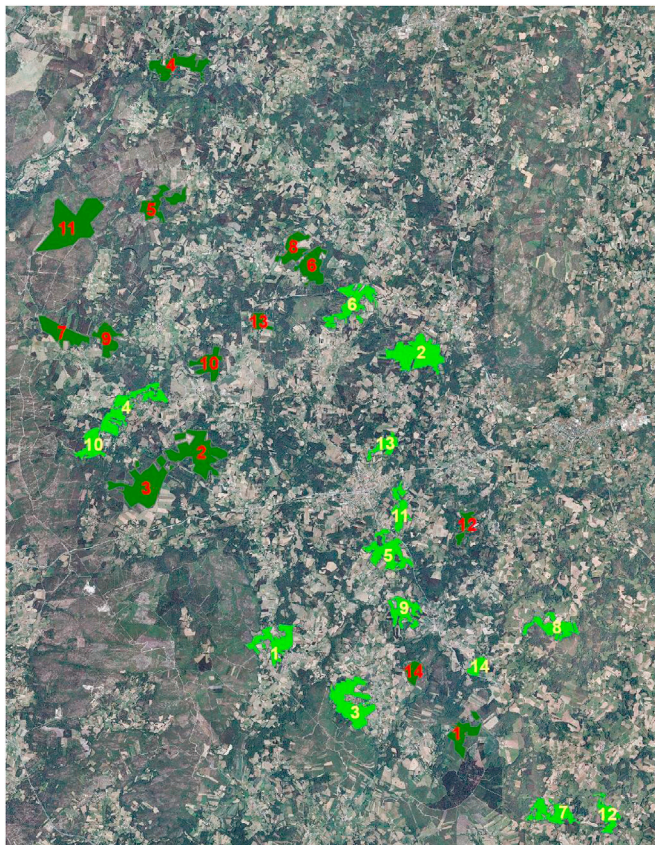
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APPENDIX A

Map of the distribution of patches in the study area, showing land cover. Dark green patches with red numbers correspond to *Eucalyptus* plantations and light green patches with yellow numbers to native forests. Numbers correspond to pairs.



APPENDIX B

Vegetation characteristics for each 14 native and 14 eucalyptus patches in the study, showing their type (Native vs *Eucalyptus*); Size (in Ha); Patch ID; Pair, distance in Km between patches of a pair ("Dist. pair (km)"); distance in metres from transect to nearest edge ("Dist. Trans. Edge"); average number of trees ("N. trees"); tree diameter at breast height in centimeters ("DBH"); tree height in metres ("Tree height"); number of species of trees ("N. sp. trees"); percentage of canopy cover ("P. can. cov."); number of species of shrubs ("N. sp. Shrub"); percentage of shrub cover ("P. cov. Shrub") and shrub height in metres ("Shrub height") in the three 20 × 20 plots for each patch.

Patch Type	Size	Patch ID	Pair	Dist. pair (km)	Dist. Trans. Edge	N. trees	Tree Diam.	Tree height	N. sp. trees	P. can. cov.	N. sp. Shrub	P. cov. Shrub	Shrub height
Native	38	14A	1	5,591	30	27.22	73.33	19.67	6	78.33	9	60.00	1.23
Eucalyptus	30	11E	1	5,591	30	533.33	40.00	10.67	1	46.67	6	40.00	0.43
Native	62	0A	2	6,608	100	19.78	25.56	19.00	5	73.33	11	56.67	0.55
Eucalyptus	70	14E	2	6,608	150	383.33	55.00	18.67	3	43.33	6	45.00	0.80
Native	58	6A	3	6,329	80	15.11	91.11	16.33	5	76.67	9	53.33	0.63
Eucalyptus	70	13E	3	6,329	150	200.00	65.00	11.67	4	41.67	5	50.00	1.02
Native	49	11A	4	7,620	100	17.78	53.33	20.67	7	68.33	13	70.00	0.50
Eucalyptus	39	9E	4	7,620	80	363.33	75.00	27.33	3	43.33	11	63.33	0.40
Native	43	3A	5	9,121	140	13.56	113.33	16.67	4	78.33	11	56.67	0.40
Eucalyptus	35	5E	5	9,121	50	280.00	100.00	20.00	3	46.67	6	53.33	0.95
Native	42	13A	6	1,334	20	12.56	71.11	17.00	8	56.67	14	56.67	1.17
Eucalyptus	33	0E	6	1,334	30	240.00	29.67	29.67	1	36.67	7	56.67	0.80
Native	32	7A	7	15,054	110	13.00	80.90	13.67	4	80.00	11	81.67	0.95

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(continued)

Patch Type	Size	Patch ID	Pair	Dist. pair (km)	Dist. Trans. Edge	N. trees	Tree Diam.	Tree height	N. sp. trees	P. can. cov.	N. sp. Shrub	P. cov. Shrub	Shrub height
Eucalyptus	33	2E	7	15,054	30	206.67	40.00	16.67	3	45.00	8	80.00	1.27
Native	30	9A	8	10,005	150	35.33	35.56	19.00	5	86.67	11	53.33	0.60
Eucalyptus	25	1E	8	10,005	40	218.67	26.67	22.50	5	40.00	6	26.67	1.03
Native	28	5A	9	8,786	100	15.22	86.67	28.00	4	78.33	10	56.67	0.86
Eucalyptus	25	4E	9	8,786	50	307.67	93.33	28.00	2	41.67	8	63.33	0.87
Native	23	1A	10	3,159	50	15.89	57.78	14.00	4	78.33	14	66.67	1.18
Eucalyptus	25	7E	10	3,159	30	286.67	33.33	11.67	2	33.33	8	70.00	0.92
Native	21	4A	11	9,413	30	26.56	100.00	22.33	3	78.33	11	81.67	0.93
Eucalyptus	17	3E	11	9,413	30	100.00	46.67	14.67	4	40.00	6	75.00	0.75
Native	19	8A	12	7,069	100	20.78	73.61	17.33	6	86.67	12	60.00	0.85
Eucalyptus	14	8E	12	7,069	40	250.67	60.00	22.33	3	30.00	6	48.33	0.60
Native	16	2A	13	4,992	60	28.11	61.11	14.67	3	80.00	9	76.67	0.87
Eucalyptus	10	12E	13	4,992	20	183.33	73.33	20.67	5	43.33	6	66.67	0.47
Native	11	12A	14	8,920	50	12.67	85.56	18.33	4	81.67	12	65.00	0.53
Eucalyptus	13	6E	14	8,920	30	123.33	40.00	14.67	4	33.33	7	70.00	1.08

APPENDIX C

Herb species observed in the study, with their corresponding phytosociological class and habitat (following [Rivas-Martínez et al., 2002](#)), being "FLP": Freshwater lakes and ponds; IGAG": Intensely grazed acidophilous grasslands; "LRS": Lithosols and rock surfaces; "MWMP": Mesophile to wet meadows and pastures; "NNP": Non nitrophilic pastures; "NSSWF": Nitrified and semi-shaded wood fringes; "NWC": Nitrophilic walls and caves; "PG": Perennial grasslands; "SC": Scrubland; "SSFE": Semi-shaded forest edges and "TDMF": Temperate deciduous or mixed forests. Together with the total number of plots in which each species was found in all native and *Eucalyptus* patches added, and the total number of patches in which each species was present, in which 28 is the maximum, as there are 14 native and 14 *Eucalyptus* patches.

Species	Phytosociological class	Habitat	Native	Eucalyptus	Num. Patches
<i>Agrostis curtisii</i>	Calluno-Ulicetea	SC	0	1	1
<i>Agrostis stolonifera</i>	Molinio-Arrhenatheretea	MWMP	4	8	10
<i>Agrostis tenuis</i>	Molinio-Arrhenatheretea	MWMP	3	6	5
<i>Anthoxanthum amarum</i>	Galio-Urticetea	NSSWF	2	0	2
<i>Arenaria montana</i>	Quercu-Fagetea	TDMF	16	23	22
<i>Arrhenatherum elatius ssp. bulbosum</i>	Molinio-Arrhenatheretea	MWMP	27	22	24
<i>Arrhenatherum longifolium</i>	Calluno-Ulicetea	SC	9	5	7
<i>Briza maxima</i>	Tuberarietea guttatae	NNP	0	3	1
<i>Centaurea nigra</i>	Trifolio-Geranietea	SSFE	0	2	2
<i>Clyнопodium vulgare</i>	Trifolio-Geranietea	SSFE	1	0	1
<i>Daboecia cantabrica</i>	Calluno-Ulicetea	SC	0	1	1
<i>Dactylis glomerata</i>	Molinio-Arrhenatheretea	MWMP	14	5	11
<i>Digitalis purpurea purpurea</i>	Carici piluliferae	NSSWF	23	5	16
<i>Galium aparine</i>	Galio-Urticetea	NSSWF	8	0	4
<i>Geranium robertianum</i>	Galio-Urticetea	NSSWF	5	3	4
<i>Gladiolus illyricus</i>	Festuco-Brometea	SSFE	0	1	1
<i>Glandora prostrata</i>	Calluno-Ulicetea	SC	7	13	12
<i>Halimium lasianthum ssp. alyssoides</i>	Calluno-Ulicetea	SC	0	18	11
<i>Holcus mollis</i>	Quercu-Fagetea sylvaticae	TDMF	35	25	25
<i>Hypochaeris radicata</i>	Molinio-Arrhenatheretea	MWMP	3	0	3
<i>Lamium maculatum</i>	Galio-Urticetea	NSSWF	1	1	2
<i>Limniris pseudacorus</i>	Magnocarici-Phragmitetea	FLP	7	2	5
<i>Lolium perenne</i>	Molinio-Arrhenatheretea	MWMP	9	12	14
<i>Malva tournefortiana</i>	Stipo giganteae-Agrostietea castellanae	PG	0	1	1
<i>Mentha spicata</i>	Molinio-Arrhenatheretea	MWMP	3	0	2
<i>Mercurialis annua</i>	Galio-Urticetea	NSSWF	10	0	7
<i>Myosotis discolor</i>	Tuberarietea guttatae	NNP	3	1	2
<i>Poa nemoralis</i>	Molinio-Arrhenatheretea	MWMP	2	1	2
<i>Polygonum persicaria</i>	Quercu-Fagetea sylvaticae	TDMF	3	0	1
<i>Potentilla erecta</i>	Nardetea strictae	IGAG	3	1	2
<i>Ranunculus repens</i>	Molinio-Arrhenatheretea	MWMP	2	0	2
<i>Scilla verna</i>	Nardetea strictae	IGAG	2	0	1
<i>Sedum acre</i>	Sedo-Scleranthetea	LRS	1	0	1
<i>Stellaria holostea</i>	Quercu-Fagetea sylvaticae	TDMF	18	3	13
<i>Teucrium scorodonia</i>	Quercu-Fagetea sylvaticae	TDMF	5	0	4
<i>Umbiliciscus rupestris</i>	Parietarietea judaicae	NWC	5	1	5

(continued)

Species	Phytosociological class	Habitat	Native	Eucalyptus	Num. Patches
<i>Urtica dioica</i>	<i>Galio-Urticetea</i>	NSSWF	2	1	2
<i>Veronica chamaedrys</i>	<i>Trifolio-Geranietea sanguinei</i>	SSFE	7	0	4
<i>Xolantha gutatta</i>	<i>Tuberarietea guttatae</i>	NNP	0	1	1

APPENDIX D

Bird species observed in the study, with their typical habitat (following EBCC, 2014), being “AG”: Agricultural; “IN”: Indetermined; “FO”: Forestal and “SH”: Scrubland; the proportional abundances in native (“Prop. Native”) and *Eucalyptus* (“Prop. Eucalyptus”) patches related to the total abundance per species; the total abundances observed per patch; together with the total number of species and abundance in each patch type.

Species	Habitat	Prop. Native	Prop. Eucalyptus	Native	Eucalyptus
<i>Accipiter nisus</i>	IN	0.00	1.00	0	3
<i>Aegithalos caudatus</i>	IN	0.92	0.08	54	5
<i>Anthus trivialis</i>	IN	0.71	0.29	24	10
<i>Buteo buteo</i>	IN	0.82	0.18	18	4
<i>Carduelis carduelis</i>	AG	0.71	0.29	5	2
<i>Carduelis chloris</i>	AG	0.58	0.42	15	11
<i>Certhia brachydactyla</i>	FO	0.97	0.03	28	1
<i>Columba palumbus</i>	FO	0.82	0.18	123	27
<i>Corvus corone</i>	AG	0.70	0.30	65	28
<i>Cuculus canorus</i>	IN	0.91	0.09	21	2
<i>Cyanistes caeruleus</i>	FO	0.97	0.03	74	2
<i>Dendrocopos major</i>	FO	0.85	0.15	40	7
<i>Emberiza cirulus</i>	AG	0.60	0.40	3	2
<i>Erithacus rubecula</i>	FO	0.73	0.27	232	87
<i>Fringilla coelebs</i>	FO	0.93	0.07	147	11
<i>Garrulus glandarius</i>	FO	0.73	0.27	61	23
<i>Hippolais polyglotta</i>	SH	0.71	0.29	5	2
<i>Lophophanes cristatus</i>	FO	0.71	0.29	42	17
<i>Motacilla alba</i>	AG	0.33	0.67	1	2
<i>Oriolus oriolus</i>	FO	0.96	0.04	26	1
<i>Parus major</i>	FO	0.91	0.09	138	13
<i>Periparus ater</i>	FO	0.79	0.21	201	52
<i>Phylloscopus ibericus</i>	IN	0.85	0.15	80	14
<i>Picus viridis</i>	IN	0.64	0.36	16	9
<i>Prunella modularis</i>	SH	1.00	0.00	2	0
<i>Pyrrhula pyrrhula</i>	FO	0.88	0.13	14	2
<i>Regulus ignicapillus</i>	FO	0.89	0.11	154	19
<i>Serinus serinus</i>	AG	0.72	0.28	13	5
<i>Sitta europaea</i>	FO	0.99	0.01	72	1
<i>Streptopelia turtur</i>	AG	0.83	0.17	49	10
<i>Sturnus unicolor</i>	AG	0.94	0.06	16	1
<i>Sylvia atricapilla</i>	IN	0.83	0.17	151	32
<i>Sylvia communis</i>	IN	1.00	0.00	1	0
<i>Troglodythys troglodythes</i>	SH	0.73	0.27	346	127
<i>Turdus merula</i>	IN	0.89	0.11	98	12
<i>Turdus philomelos</i>	FO	0.91	0.09	40	4
<i>Turdus viscivorus</i>	FO	1.00	0.00	7	0
<i>Upupa epops</i>	AG	1.00	0.00	2	0
Total Num sp.				37	34
Total Abund.				2384	548

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