



Original article

Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal

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ABSTRACT

Forest ecosystems have been subjected to continuous dynamics between deforestation and forestation. Assessing the effects of these processes on biodiversity could be essential for conservation planning. We analyzed patterns of species richness, diversity and evenness of plants and birds in patches of natural forest of *Quercus* spp. and in stands of native *Pinus pinaster* and exotic *Eucalyptus globulus* in NW Portugal. We analyzed data of forest and non-forest species separately, at the intra-patch, patch and inter-patch scales. Forest plant richness, diversity and evenness were higher in oak forest than in pine and eucalypt plantations. In total, 52 species of forest plants were observed in oak forest, 33 in pine plantation and 28 in eucalypt plantation. Some forest species, such as *Euphorbia dulcis*, *Omphalodes nitida* and *Eryngium juresianum*, were exclusively or mostly observed in oak forest. Forest bird richness and diversity were higher in both oak and pine forests than in eucalypt forest; evenness did not differ among forests. In total, 16 species of forest birds were observed in oak forest, 18 in pine forest and 11 in eucalypt forest. Species such as *Certhia brachydactyla*, *Sitta europaea* and *Dendrocopos major* were common in oak and/or pine patches but were absent from eucalypt stands. Species-area relationships of forest plants and forest birds in oak patches had consistently a higher slope, at both the intra and inter-patch scales, than species-area relationships of forest species in plantations and non-forest species in oak forest. These findings demonstrate the importance of oak forest for the conservation of forest species diversity, pointing the need to conserve large areas of oak forest due to the apparent vulnerability of forest species to area loss. Additionally, diversity patterns in pine forest were intermediate between oak forest and eucalypt forest, suggesting that forest species patterns may be affected by forest naturalness.

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1. Introduction

Forests provide a range of ecosystem services (Shvidenko et al., 2005). Due to their direct use and market value, forest goods, in particular wood, have been the object of more demand than other benefits provided by forests, such as soil stabilization (Liu and Diamond, 2005), climate regulation (Malhi et al., 2008) or biodiversity (Barlow et al., 2007). This bias has contributed to two processes of land use change: the loss and fragmentation of native forests and the establishment and maturation of new plantation forests (Ciancio and Nocentini, 1997; FAO, 2006). Production targets instead of conservation targets have often shaped these new forests (Ciancio and Nocentini, 1997; Koch and Skovsgaard, 1999; FAO, 2006), which are frequently monocultures often composed of introduced species and even-aged trees, a design that generally does not promote biodiversity (Hartley, 2002). Because biodiversity has a key role in

sustaining ecosystem services and promoting ecosystem resilience (MA, 2005), production forests with low biodiversity tend to be more vulnerable to disturbance and environmental change than natural forests (Lugo, 1997; Carnus et al., 2006; Bassi et al., 2008).

In a world facing fast environmental changes, the role of forest ecosystems for conservation, as reservoirs of biodiversity and providers of multiple ecosystem services, is of unquestionable importance (Shvidenko et al., 2005). Recent forecasts indicate that land use change will be the main cause of biodiversity loss in the next decades (van Vuuren et al., 2006). Therefore, understanding the effects of land use changes, namely forest loss and forest plantation, on the diversity of forest species is fundamental for conservation planning.

In Portugal, forest cover was once dominated by oak species (*Quercus* spp.). In broad terms, deciduous species, such as the common oak (*Quercus robur*) were dominant in the northern half of the country and evergreen species, such as the cork oak (*Quercus suber*), in the southern half. While evergreen oaks are still abundant in the south, mainly due to their economical value (e.g. cork production), in the north, deciduous oaks present a scattered

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distribution and represent only 4% of the country forest (Ramil-Rego et al., 1998; DGRF, 2007). However, these natural forests of *Q. robur* and *Quercus pyrenaica* are acknowledged by their value as providers of several ecosystem services being listed in the Annex I of the Habitats Directive (ICN, 2006).

In contrast, pine (*Pinus pinaster*) and eucalypt (*Eucalyptus globulus*) account nowadays for more than 40% of the country forest and dominate the northern half of the country (DGRF, 2007). *P. pinaster* is a native species, but its distribution has been expanded and modified by plantation development. *E. globulus* is an exotic species, originally from southeastern Australia.

Here, we investigate the role of deciduous oak forest (natural forest, native species), pine forest (planted forest, native species) and eucalypt forest (planted forest, exotic species) for the conservation of forest plants and birds. We follow a multi-scale and multi-taxa approach to the analysis of species diversity patterns in the three forest types. We analyze species diversity at three spatial scales: sample unit scale, patch scale and study area scale; and species-area relationships (SAR) at two spatial scales: intra-patch and inter-patch. We test the relevance of oak forest for forest plants and forest birds following two complementary pathways: through the comparison of SAR of forest species in the three types of forest and through the comparison of SAR of forest species versus non-forest species in oak forest.

We hypothesize that diversity of plant and bird forest species will be affected by the degree of forest naturalness (i.e., the degree to which an area is free of human influence or, the successional proximity of the vegetation to the historical natural conditions (Boteva et al., 2004)) and that these forest species will be particularly vulnerable to the loss of natural forest. More specifically, and focusing on forest species, we predict that: (i) forest species diversity will be higher in oak forest patches (natural forest, higher naturalness), while pine stands (native plantation, intermediate naturalness) will be less diverse than oak patches but more than eucalypt stands (exotic plantation, lower naturalness); (ii) forest species diversity will be more associated with patch size in natural forest than in planted forests, due to the degree of forest naturalness (i.e., if forest species are better adapted to the conditions found in natural forests; an increase in niche availability, due to area increase, will promote an increase in species diversity), and (iii) forest species diversity will be more associated with patch size in natural forest than non-forest species diversity, due to species habitat specificity, but differences between taxa will be less evident, if existent, in planted forests.

2. Methods

This study was conducted in the Alto Minho region in NW Portugal (41°N 8°W) (Fig. 1). The landscape is mainly composed of shrubland, agricultural fields and forest, mainly pine, eucalypt and oak (DGRF, 2007). We selected patches of oak forest (*Q. robur* and *Q. pyrenaica*) and stands of pine and eucalypt according to the following criteria: forest composed of adult trees, with a close canopy (>30% cover) and isolated from other forest patches by a matrix of shrubland or agriculture. The size of forest patches ranged from 0.22 ha to 36.52 ha (Table 1). The area of the patches was calculated from orthophotomaps using ArcGIS 9.0 software.

We defined as sample unit a square of 10 m × 10 m (100 m²). Plants were sampled in five sub-units of 1 m × 1 m (1 m²). The abundance of plants in each sample unit was ranked from 0 to 5, depending on the number of sub-units where the species was found. The sampling effort was proportional to a species-area relationship, $U = A^{0.33}$, where U is the number of sub-units and A the area (m²) of the patch. The number of sample units (see Table 1) was the integer part of U/5. We chose the value 0.33 as the exponent because it was within the proposed range of values for isolated areas ($0.25 < z < 0.35$) (Rosenzweig, 1995), and resulted in a feasible sampling effort. Moreover, this exponent agrees with the mean value of z found for isolated areas by van Vuuren et al. (2006). The use of a proportional sampling scheme (i.e. maintaining sample size proportional to site dimension) may provide a more precise approach to the study of the effects of area on species diversity than other sampling designs (Schoereder et al., 2004). Using a proportional sampling effort reduces the probability of missing a given habitat (or habitat feature) inside a patch as the area increases, therefore reducing the probability of missing species that use that habitat (Schoereder et al., 2004).

Sample units were arranged in a way that maximized the distance between them, while maintaining a buffer of at least 15 m from the edge. Data were collected during July and August 2005.

Plants were identified at the species level whenever possible, and were classified as either forest or non-forest plants. The classification followed the species ecological information in Honrado (2003). We followed an inclusive classification of forest plants, accepting every species that was reported to appear in forest environments.

Summer bird populations were surveyed through 15-min point counts at the centre of each sample unit. Bird data were collected during the first 3 h of the day and never under rainy conditions.

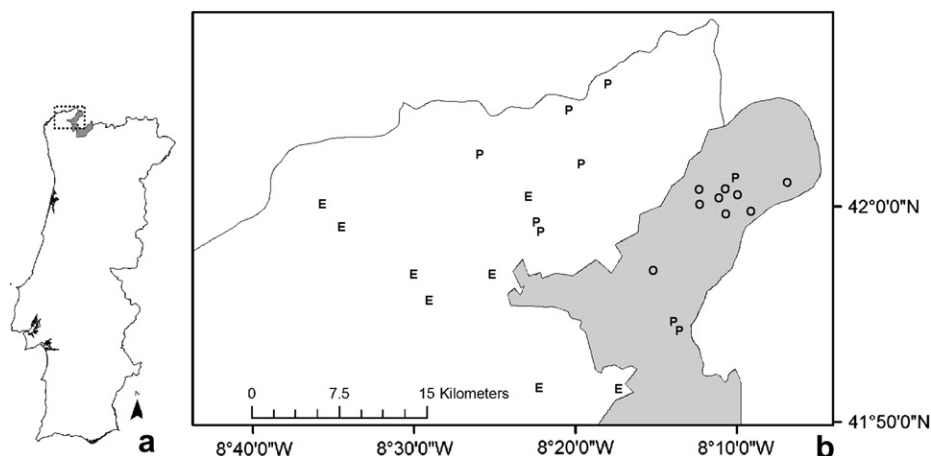


Fig. 1. Location of the study area in Portugal (ca. 40 km × 25 km, limited by the dotted frame) (a); Distribution of forest patches within the study area (O – oak, P – pine, E – eucalypt) (b). The region in grey represents the National Park of Peneda-Gerês.

Table 1

Patches data and diversity measures by taxa: area, perimeter-area ratio (PAr), number of sample units (SU), species richness (N), Shannon–Wiener diversity (H') and evenness (J). The total number of species from each taxa found in each forest type is presented in the row preceding patches data.

	Area (ha)	PAr	SU	Forest plants			Non-forest plants			Forest birds			Non-forest birds		
				N	H'	J	N	H'	J	N	H'	J	N	H'	J
<i>Oak forest patches</i>				52			32			16			11		
O1	0.39	4.10	3	18	2.55	0.88	11	1.98	0.83	5	1.33	0.83	4	1.16	0.83
O2	1.22	4.33	4	27	3.09	0.94	10	2.04	0.88	4	1.23	0.89	6	1.67	0.93
O3	2.20	5.94	5	26	2.96	0.91	16	2.51	0.90	6	1.60	0.89	9	1.89	0.84
O4	2.85	4.10	5	24	2.82	0.89	6	1.38	0.77	8	1.99	0.96	6	1.44	0.81
O5	3.36	4.84	6	25	2.83	0.88	10	1.64	0.71	9	2.00	0.91	5	1.48	0.92
O6	5.19	7.56	7	28	3.03	0.91	16	2.35	0.85	9	1.71	0.78	9	1.71	0.77
O7	6.00	4.75	7	32	3.06	0.88	8	1.50	0.72	12	2.13	0.86	8	1.79	0.86
O8	10.30	5.75	9	37	3.24	0.90	14	1.84	0.70	15	2.35	0.87	9	1.81	0.82
O9	21.66	6.45	11	26	2.81	0.86	13	2.24	0.87	10	1.96	0.85	8	1.75	0.84
<i>Pine forest patches</i>				33			28			18			17		
P1	0.22	4.04	2	8	1.76	0.85	8	1.80	0.87	3	0.86	0.78	8	1.73	0.83
P2	0.53	4.25	3	11	2.11	0.88	9	1.90	0.86	4	1.28	0.92	7	1.80	0.93
P3	1.01	5.86	4	10	1.93	0.84	7	1.73	0.89	10	2.15	0.93	6	1.64	0.91
P4	2.83	4.67	5	14	2.01	0.76	10	1.95	0.85	8	1.95	0.94	7	1.88	0.96
P5	4.76	5.75	6	11	1.95	0.81	8	1.47	0.71	8	1.65	0.79	7	1.69	0.87
P6	8.62	5.16	8	20	2.43	0.81	21	2.56	0.84	8	1.73	0.83	7	1.69	0.87
P7	11.91	5.81	9	14	2.08	0.79	11	1.47	0.61	10	2.12	0.92	6	1.59	0.89
P8	15.98	5.86	10	10	1.52	0.66	5	1.18	0.73	11	2.05	0.86	9	1.88	0.86
P9	31.09	4.30	12	13	2.14	0.83	5	1.03	0.64	9	1.86	0.85	6	1.63	0.83
<i>Eucalypt forest patches</i>				28			21			11			13		
E1	0.62	3.81	3	4	1.20	0.87	4	1.37	0.99	4	1.10	1.00	2	0.69	1.00
E2	1.19	4.77	4	8	1.50	0.72	9	1.88	0.85	2	0.56	0.81	4	1.21	0.87
E3	1.89	4.52	5	14	2.18	0.83	9	1.98	0.90	5	1.35	0.84	7	1.66	0.75
E4	2.76	5.29	5	8	1.82	0.87	9	1.76	0.80	4	1.12	0.81	5	1.29	0.80
E5	5.62	5.25	7	7	1.72	0.88	9	1.81	0.82	6	1.72	0.96	5	1.23	0.77
E6	7.92	8.29	8	5	1.20	0.75	9	1.83	0.83	6	1.61	0.90	5	0.95	0.48
E7	18.81	5.29	11	12	1.53	0.62	13	1.95	0.76	4	1.26	0.91	5	0.94	0.58
E8	36.52	4.41	13	15	2.18	0.80	12	2.01	0.81	6	1.52	0.85	7	1.50	0.77

Birds were visually and acoustically identified in a range of up to 25 m. The data relative to birds of prey, owls, swifts, swallows and nightjars were excluded from the analyses (but are presented in Table A2, Supplementary material) because the method of survey is not the adequate to sample these species (Bibby et al., 2000). Birds were classified either as forest or non-forest species according to their habitat requirements: forest species nest within forests, whereas non-forest species can nest outside forests. The classification followed the species ecological information in Pimenta and Santarém (1996). The criterion used in bird classification was more restrictive than the criterion used for plants (i.e., a plant species only had to be reported to occur in forests to be classified as a forest species). This difference in criteria was due to the type of information on species habits available at the regional level (the Peneda-Gerês National Park). This factor will be taken in consideration in the discussion.

All subsequent analyses were performed considering each of the four groups described above: forest and non-forest plants, forest and non-forest birds. The separate analysis by groups of species was recommended in other species-area studies due to possible differences in the response of the groups (Godefroid and Koedam, 2003; Magura et al., 2008). Moreover, this approach may contribute to a more accurate assessment of the effect of land use change on native species in countryside landscapes where native and non-native habitats coexist (Pereira et al., 2004; Pereira and Daily, 2006).

We compared the mean diversity of each taxon in each forest type using three measures of diversity: species richness, species diversity (Shannon–Wiener diversity index, $H' = -\sum_{i=1}^S p_i \ln p_i$) and evenness ($H/\ln(S)$). These measures were determined for each patch and covariance analyses were performed to test for a possible interactive effect between patch area (continuous covariate) and forest type, as well as to detect the effect of patch area alone.

We found no interactive effect between the variables and we only found an isolated effect of area (and no effect of forest type) on the evenness of non-forest plants. Having these results in consideration, we opted to use one-way ANOVAs and post-hoc Tukey's HSD to test for differences in the mean values of species richness, species diversity and evenness. Data assumptions were verified prior to the tests.

Mean species richness of sample units was compared between forest types using the Welch test, an alternative to ANOVA recommended when homoscedasticity is not verified (Grissom, 2000; Quinn and Keough, 2002). Posterior pairwise comparisons were performed using the t test (p value adjusted by the Holm's method).

We studied species–area relationships (SAR) using the power model (Arrhenius, 1921), $S = c A^z$, and the exponential model (Gleason, 1922), $S = c + z \log(A)$, where S is the number of species, A is the area and c and z are parameters of the model. Some studies suggested that the power model is a better choice for intermediate and larger scales of analysis, whereas the exponential model, or semi-log, would perform better at small scales of analysis (Tjørve, 2003; Rosenzweig, 1995). Moreover, Ugland et al. (2003) also suggested that the semi-log model should be preferred when dealing with species-accumulation data, i.e. species increase due to accumulation of equal sized samples within a habitat.

We evaluated the adjustment of species–area data to the power model (on its log–log form, $\log S = c + z \log A$) and to the exponential model through the comparison of residuals distribution and the value of r^2 . The power model was overall better adjusted to species–area data at the inter-patch level (study area level), with the exponential model being only slightly better for eucalypt stands data. At the intra-patch scale all SAR were significant ($p > 0.05$) and better adjusted to the semi-log model. Species data used to test intra-patch SAR were $\log(x+1)$ transformed (power model) and $(x+1)$ transformed (exponential model).

Intra-patch SAR were calculated for plants using data from three sample scales: 1 m², 100 m² and the patch area. A two-way ANOVA and the post-hoc Tukey's HSD were used to compare the z' values of intra-patch SARs (the ANOVA assumptions were verified). Forest type and species group were set as factors.

The influence of perimeter-area ratio (perimeter/ $\sqrt{\text{area}}$) on species richness was analyzed through simple linear regression. We used the perimeter-area ratio as a measure of the extent of forest edge. The independence between area and perimeter-area ratio was tested through Pearson's correlation coefficient. Statistical analyses were performed using the R statistical software system (www.cran.r-project.org) and the values of Shannon–Wiener diversity were determined using the EstimateS software (Colwell, 2005).

3. Results

During this study we recorded 106 plant taxa (see Supplementary material Table A1). Some plants could not be identified at the species level. Because all records in the species list correspond to different taxonomic units, they were used as different species in data analysis, and hereafter will be referred to as species. At the study area level, we found 52 forest plant species in oak forest, 33 in pine forest and 28 in eucalypt forest, and, in the same order, 32, 28 and 21 species of non-forest plants (Table 1). Some forest plants only, or mainly, occurred in oak forest, in some cases being present in most of the patches. Examples include *Crepis lampanoides*, *Euphorbia dulcis*, *Asphodelus lusitanicus*, *Melampyrum pratense*, *Omphalodes nitida* and *Eryngium juresianum*. In addition, species such as *Lithodora prostrata*, *Lonicera periclymenum*, *Potentilla erecta* and *Viola lactea* were mainly observed in native plant communities (i.e., oak and pine). A third group of plants was mainly observed in plantations (i.e., pine and eucalypt). Examples include *Erica umbelata*, *Ulex europaeus*, *Calluna vulgaris* and *Hypericum linarifolium*.

With respect to birds, we recorded 38 species (see Supplementary material Table A2). We found 16 forest bird species in oak forest, 18 in pine forest and 11 in eucalypt forest, and, in the same order, 11, 17 and 13 species of non-forest birds (Table 1). According to our records some species were common in oak and pine forest but not in eucalypt forest: *Sitta europaea* was only observed in oak forest, *Dendrocopus major* in pine forest and *Certhya brachydactyla* and *Fringilla coelebs* both in oak and pine forest.

At the patch level, forest plant richness, diversity and evenness were higher in oak forest than in pine and eucalypt plantations (Table 2). Non-forest plant richness, diversity and evenness were not significantly different among forest types. Mean values of richness and diversity of forest birds and non-forest birds in oak forest were similar to mean values in pine forest and higher than in eucalypt forest. The evenness of forest birds did not differ among forest types, and the evenness of non-forest birds did not differ between oak forest and plantations.

At the sample unit level (100 m²), mean species richness differed among forest types for all species groups: forest plants ($F_{2,106} = 180.21$, $p < 0.001$), non-forest plants ($F_{2,108} = 6.37$, $p < 0.05$), forest birds ($F_{2,101} = 53.1$, $p < 0.001$) and non-forest birds ($F_{2,111} = 13.6$, $p < 0.001$). Results from pairwise comparisons indicated that the mean richness of forest plants was different among all pairs of forests ($p \text{ adj} < 0.01$). Oak forest presented the highest mean, followed by pine and then eucalypt. Regarding the mean richness of non-forest plants, the only difference was found between eucalypt and pine sample units ($p \text{ adj} = 0.01$). Eucalypt sample units were the richest in non-forest plants, while pine sample units were the poorest. In terms of forest and non-forest bird species at the sample unit level, there were differences among all pairs ($p \text{ adj} < 0.05$). Oak sample units were the richest in both forest and non-forest birds being followed by pine sample units. Sample units in eucalypt forests were the least rich.

Table 2
Comparison of species richness, species diversity and evenness of forest and non-forest species in patches of oak, pine and eucalypt forest. Significant results with $p < 0.05$, ns – not significant. Pairwise comparisons: O – oak, P – pine, E – eucalypt; Tukey HSD, $p < 0.05$ *, < 0.01 **, < 0.001 ***.

	n	Species richness		Species diversity		Evenness	
		Mean	SE	Mean	SE	Mean	SE
<i>Forest plants</i>							
Oak patches	9	27.00	1.76	2.93	0.07	0.89	0.01
Pine patches	9	12.33	1.17	1.99	0.08	0.80	0.02
Eucalypt patches	8	9.12	1.44	1.67	0.14	0.79	0.03
F-value (2,23), p <		41.68	0.05	45.82	0.001	6.46	0.01
Post-hoc comparisons		O vs. P, E *** P vs. E ^{ns}		O vs. P, E *** P vs. E ^{ns}		O vs. P* O vs. E ** P vs. E ^{ns}	
<i>Non-forest plants</i>							
Oak patches	9	11.56	1.16	1.94	0.13	0.80	0.03
Pine patches	9	9.33	1.61	1.68	0.15	0.78	0.03
Eucalypt patches	8	9.25	0.94	1.82	0.07	0.85	0.03
F-value (2,23), p <		1.04	ns	1.16	ns	1.29	ns
Post-hoc comparisons		all comparisons ^{ns}		all comparisons ^{ns}		all comparisons ^{ns}	
<i>Forest birds</i>							
Oak patches	9	8.67	1.15	1.81	0.12	0.87	0.02
Pine patches	9	7.89	0.90	1.74	0.14	0.87	0.02
Eucalypt patches	8	4.50	0.53	1.28	0.13	0.88	0.02
F-value (2,23), p <		5.50	0.05	4.53	0.05	0.16	ns
Post-hoc comparisons		O vs. P ^{ns} O, P vs. E ⁺		P vs. O, E ^{ns} O vs. E ⁺		all comparisons ^{ns}	
<i>Non-forest birds</i>							
Oak patches	9	7.11	0.63	1.63	0.01	0.85	0.02
Pine patches	9	7.00	0.33	1.73	0.04	0.89	0.01
Eucalypt patches	8	5.00	0.57	1.18	0.11	0.78	0.05
F-value (2,23), p <		4.91	0.05	13.08	0.001	3.56	0.05
Post-hoc comparisons		O vs. P ^{ns} O, P vs. E ⁺		O vs. P ^{ns} O vs. E ^{**} P vs. E ^{***}		O vs. P, E ^{ns} P vs. E ⁺	

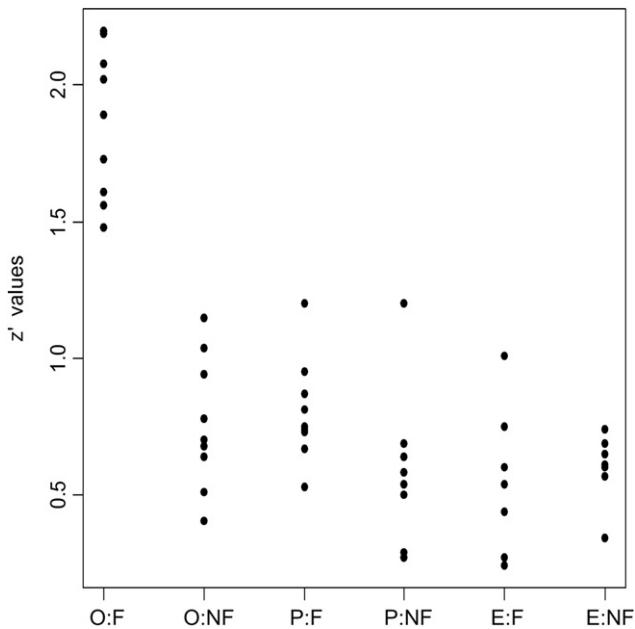


Fig. 2. Magnitude of z' values of intra-patch species–area relationships by forest type and plants habitat specificity. Horizontal axis: oak (O), pine (P), eucalypt (E), forest species (F), non-forest species (NF).

A two-way ANOVA tested for the effect of forest type ($F_{2,46} = 50.4, p < 0.001$), taxon ($F_{1,46} = 44.37, p < 0.001$) and also an interaction between these factors ($F_{2,46} = 30.33, p < 0.00001$) on the z' values of intra-patch SAR. Results from pairwise comparisons indicate that the mean z' value of forest plant species in oak patches was significantly different (Tukey HSD, $p < 0.001$) from the mean z' value of each of the other pairs “forest type: species group” (Fig. 2).

At the study area level, we found significant species–area relationships for forest plants, forest birds and non-forest birds in oak forest, for forest birds in pine forest and for non-forest plants in eucalypt forest (Table 3, Fig. 3). The extent of the forest edge was correlated with the richness of non-forest plants ($r^2 = 0.67, p < 0.05$) and non-forest birds ($r^2 = 0.59, p = 0.01$) in oak forest patches, and with forest bird richness ($r^2 = 0.61, p = 0.01$) in pine stands. Perimeter–area ratio and area varied independently in all forest types.

4. Discussion

4.1. Forest species diversity by forest type

The higher richness and diversity of forest species found in natural forest is in agreement with other studies that also

Table 3 Inter-patch species–area relationships ($\log S = c + z \log A$). Significant regressions: $p < 0.05$, ns – not significant.

	Plants					Birds				
	n	z	c	r ²	p<	z	c	r ²	p<	
Oak: Total	9	0.09	2.7	0.40	ns	0.24	0.23	0.77	0.01	
Oak: Forest	9	0.12	2.0	0.49	0.05	0.29	-1.00	0.67	0.01	
Oak: Non-forest	9	0.05	1.8	0.04	ns	0.18	0.04	0.52	0.05	
Pine: Total	9	0.06	2.5	0.09	ns	0.08	1.80	0.57	0.05	
Pine: Forest	9	0.09	1.5	0.32	ns	0.21	-0.25	0.64	0.01	
Pine: Non-forest	9	-0.03	2.4	0.01	ns	-0.01	2.10	0.03	ns	
Eucalypt: Total	8	0.20	0.74	0.48	ns	0.18	0.31	0.52	0.05	
Eucalypt: Forest	8	0.18	0.13	0.30	ns	0.18	-0.52	0.42	ns	
Eucalypt: Non-forest	8	0.20	0.02	0.64	0.05	0.19	-0.43	0.43	ns	

compared communities in natural forest and in forest plantations (Bongiorno, 1982; Pina, 1989; Tellería and Galarza, 1990; Kwok and Corlett, 2000; Lindenmayer et al., 2003; Aauri et al., 2004; Zurita et al., 2006). The value of natural forest for conservation is further strengthened by the presence of exclusive, or nearly exclusive, forest species, as these species may be particularly vulnerable to the loss of natural forest or to forest degradation. *Omphalodes nitida* and *Eryngium juresianum* constitute two good examples, both species are endemics of the NW of the Iberian Peninsula (Castro et al., 2001; Honrado, 2003), in addition the latter species is considered to be critically endangered (Moreno, 2008). In contrast, the group of plants that occurred preferently in plantations was composed by non-forest species. Similarly, some forest birds were exclusively or mainly observed in oak forest and in pine forest. Both oak and pine forests appeared to be important habitats for forest birds. In contrast, eucalypt stands had the lowest species richness and diversity for both plants and birds.

Differences between natural and planted forests may be explained through forests naturalness and forest dynamics. Oak forest patch composition results from a dynamic relationship between fragmentation and later natural regeneration of native forest communities. In general terms, forest fragmentation probably started around 5500 BP (according to pollinic studies that detected the first signs of human intervention in this area) and continued until the 19th century (Ramil-Rego et al., 1998; Sobrino et al., 2001; Honrado, 2003). Forest regeneration has been the dominant trend in the last five decades as human rural populations have declined and migrated to urban centres (Moreira et al., 2001). Despite past and present anthropic impacts (e.g. fire), that drove most of the remaining oak forest to a pre-climatic state, oak forest patches still provide a suitable environment for the occurrence and persistence of forest species (ICN, 2006).

Pine and eucalypt forests on the other hand were planted. The communities of planted forests result from the assemblage of species formerly present in the area plus colonizers from neighbouring areas (Michelsen et al., 1996; Christian et al., 1998; Díaz et al., 1998). When planted forests are managed to meet production targets they may fail to provide the adequate conditions for the establishment or persistence of more sensitive species (Endels et al., 2004; Fraterrigo et al., 2005). For instance, species such as *Sitta europea* or *Dendrocopus major* that nest in trees holes and thus depend on the existence of old trees and large trunks for nesting (Carrascal and Tellería, 1990; Matthysen, 1998). The simplified structure of monoculture forest stands or the short rotation period that limits community assemblage, may also be the causes for the lower richness of forest birds found in planted forests (Tellería and Galarza, 1990; Kwok and Corlett, 2000; Moreira et al., 2003; Zurita et al., 2006; Magura et al., 2008). On the other hand, if correct management options are applied, planted forests, namely pine stands, may provide a good habitat to native species (Aauri et al., 2004). Conversely, the composition of natural forests may be negatively affected by human use. Santos et al. (2006), working in central Spain, reported a higher diversity of birds in large mature pine plantations than in large patches of natural forest of holm oak (*Quercus ilex*). In their study area, holm oak patches were much degraded (i.e. less natural) due to long-lasting human perturbation.

Another reason that may also explain differences in the richness of birds, in particular forest birds, between forest types is the availability of food, a factor that can also be related with forest structure. The phenology of *E. globulus* is not synchronized with the demands of native fauna. *E. globulus* flowers during the winter therefore failing to provide enough and adequate food resources to native birds in spring and summer (Tellería and Galarza, 1990). In contrast, mature pine forests may provide several food sources for

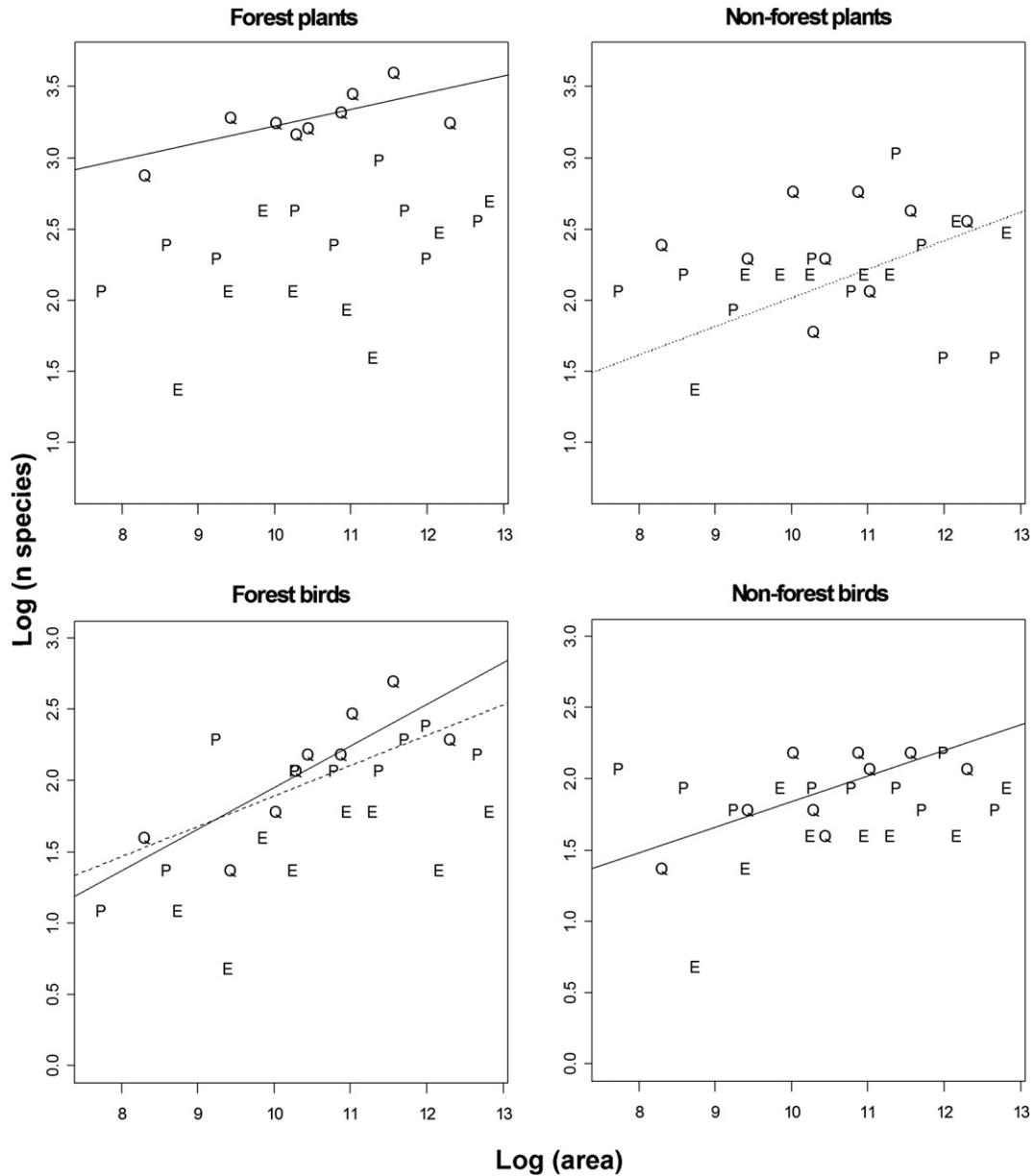


Fig. 3. Species-area relationships of forest species and non-forest species at the inter-patch level. Points: oak patches (O), pine patches (P) and eucalypt patches (E). The regression line is presented for significant relationships. Forest plants: oak (solid line). Non-forest plants: eucalypt (dotted line). Forest birds: oak (solid line), pine (dashed line). Non-forest birds: oak (solid line). Species-area parameters are presented in Table 3.

forest birds, from arthropods present in pine needles to arthropods present in shrubs and in the soil (Carrascal and Tellería, 1990).

4.2. SARs of forest species by forest type

Results from species-area analyses provided evidence on the vulnerability of forest species to the loss of natural forest. Intra-patch SAR of forest plants in oak patches had consistently higher z' values than the other tested SAR. This result has implications for conservation because the higher the slope, the stronger the association between plant richness and area. Moreover, results from intra-patch SAR were supported by results at the regional scale. Inter-patch SAR of forest plants and forest birds in oak forest were both significant and stronger than SAR in planted forests confirming the relevance of patch size for species richness in oak forest.

This finding is relevant because while intra-patch SAR curves necessarily express a non-decreasing relationship between area and the number of species, inter-patch SAR curves are not under such constraint (Scheiner, 2003).

The steeper slopes of SAR of forest plants and birds in oak forest suggest that forest species may be particularly vulnerable to the loss of natural forest and also that larger areas of natural forest are important for forest species. For example, some of the forest birds recorded in this study, namely *Aegithalos caudatus*, *Ficedula hypoleuca*, *S. europaea* and *Phylloscopus ibericus* were not observed in the smaller oak forest patches (<2.85 ha). These species may require a minimum area of forest to occur, either because they need a minimum diversity of habitats or because they use scarce resources (e.g. decrepit trees) whose availability is limited in smaller patches (Tellería and Santos, 1995; Herrando and Brotons, 2002).

The importance of large native forest patches (>100 ha) for maintaining forest avifauna has also been noted by Brotons and Herrando (2001), Santos et al. (2002), and Magura et al. (2008).

Our results from species-area analysis are in agreement with Magura et al. (2008), who also report a significant SAR of forest specialist birds in native forest patches but not in exotic stands in Hungary. The authors suggest that the forest structure, namely spatial heterogeneity within patches and the distinctive structure of native forest patches in relation to the matrix, is a relevant factor explaining differences in SAR.

Finally, we found insular z values for forest birds in oak patches but not for forest plants. Forest plants had lower z values, typical of mainland areas ($0.13 < z < 0.18$ (Rosenzweig, 1995)). Results were probably affected by the criteria used in the classification of forest plants, which categorized as forest species all the species reported to occur in forests independently of their occurrence in other type of habitats. Therefore, some of the species classified as forest plants may also occur in the surrounding matrix, being distributed according to a mainland pattern instead of an insular pattern.

4.3. SARs of forest species versus non-forest species

The stronger relationship between area and species richness of forest plants and birds in natural forest, in comparison with non-forest species, provides further evidence of the relevance of natural forest for forest species conservation. Additionally, while the number of forest species was only related to area in oak fragments, the richness of non-forest plants and non-forest birds was related with the extent of the patch edge, suggesting the occurrence of edge effects (Saunders et al., 1991; Murcia, 1995), corresponding to the flux of species from the matrix. The richness of non-forest birds was also related with area, probably due to their mobility that enables the dispersion throughout the fragment. In pine stands the richness of forest birds was related with forest area and edge extent, suggesting that while forest birds use pine stands their presence is on the one hand limited by stands size and on the other hand by the extension of forest edge, which allows species colonization from outside areas. In eucalypt stands, only non-forest plants and total bird richness presented a significant relationship with patch size which was probably due to an increase in the sampling effort, and not to species sensitivity to habitat characteristics.

5. Conclusion

Our results documented the importance of oak forest patches for the conservation of forest plants and birds. Oak forest supported a higher diversity of forest species, together with pine forest in the case of forest birds, at all scales of analysis. The association between forest species richness and patch area was always stronger in oak forest. In addition, forest naturalness seemed to influence forest species diversity, with pine stands presenting an intermediate response in relation to oak and eucalypt forests. Therefore, we reinforce the priority value for conservation of natural oak forests and the need to maintain or increase their present level of naturalness, either through the prevention of ecosystem degradation (e.g. recurrent fires, invasive species) or through the support of natural regeneration and succession in disturbed forest patches.

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Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.actao.2010.01.002

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