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Response of bird communities to silvicultural thinning of Mediterranean maquis

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Summary

1. Woodland management should consider biodiversity conservation world-wide. Landowners in some European Mediterranean regions receive subsidies to thin dense maquis. This practice eliminates most shrubs and saplings while the tallest trees are pruned to produce more open woodland stands. We investigated the impact of this practice on the conservation status of bird communities.
2. We designed a large-scale 'natural experiment' that included 21 paired thinned and unthinned maquis stands in central Spain. Every stand was sampled by means of five point counts, each consisting of a 50-m radius plot, in two consecutive years and in winter and spring. The vegetation structure was characterized after bird censuses in 10-m radius plots that coincided with the centres of the bird point counts. Data analyses were based on repeated-measures ANOVAS.
3. Thinning was responsible for a significant increase in species richness, but did not have any effect on total bird density. The average body mass of species in thinned stands was significantly larger than in unthinned, more densely vegetated, stands. The density of ground searchers was indistinguishable in thinned and unthinned stands, whereas the density of foliage gleaners was higher in unthinned stands. The winter density of granivorous species was marginally higher in thinned stands, whereas insectivorous and frugivorous species were marginally more abundant in unthinned stands.
4. Thinned areas were occupied by higher densities of bird species whose European conservation status is of high concern. Winter density of gamebirds was also higher in thinned stands.
5. *Synthesis and applications*. This is the first time that a large-scale experimental manipulation of habitat structure and vegetation volume has demonstrated the predicted allometric effect of habitat structural complexity on the average body mass of a bird community. Thinning of dense Mediterranean woodland enhanced habitat heterogeneity and suitability for several bird species and increased species richness. It was also beneficial for species of conservation concern and for non-threatened gamebirds. However, some unthinned patches should be preserved to provide refuge for the few species that are impacted by thinning.

Key-words: body mass, conservation status, density, gamebirds, guilds, species richness, vegetation structure

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Introduction

It has long been recognized that the structural complexity of vegetation influences the structure of bird communities, including the number and diversity of niches, local abundance and guilds or groups of species that exploit similar resources (Wiens 1989; Díaz *et al*. 1998). Human activities may profoundly modify land cover and the architecture of vegetation and, consequently, may affect the composition and abundance of bird species (Blondel & Aronson 1999; Heikkinen *et al*. 2004). For example, in many Mediterranean regions there has been secular clearing and thinning of the Mediterranean maquis that has turned vast expanses of dense shrubland and woodland into more open forests or human-made savannas such as the 'dehesas' (Grove & Rackham 2001; Maldonado *et al*. 2002). In this study, we investigated for the first time how the thinning of the Mediterranean maquis affects bird communities.

Since 1990, land owners in some European Mediterranean regions have received subsidies to thin dense maquis. The subsidies aim to provide environmental services and local income. This practice consists of eliminating most shrubs and saplings, and pruning the tallest trees to produce more open woodland stands. Thinning reduces competition among overstorey trees and increases penetration of solar radiation to the forest floor, thereby increasing the growth, size, branch diameter and crown ratio of remaining trees and stimulating the development of understorey vegetation (Ducrey & Toth 1992; Perevolotsky & Haimov 1992; Kaplan & Gutman 1996; Homyack, Harrison & Krohn 2004). This type of management aims to prevent fire, improve habitat conditions for game mammals (e.g. rabbit and deer) and, to a lesser extent, create pastures for extensive sheep and cattle grazing and produce firewood. It may also increase structural complexity and improve the habitat for several vertebrate species of wildlife (Sullivan, Sullivan & Lindgren 2001; Patriquin & Barclay 2003). The potential of thinning to redirect the developmental trajectory of young stands towards stands with a higher structural diversity has gained overall recognition during the last decade (DeBell *et al*. 1997).

Several studies in different ecosystems have addressed the question of how forest management affects vegetation structure (Marañón *et al*. 1999; Thomas, Halpen & Falk 1999) and the associated effects on the community structure of different taxonomic groups (Sullivan, Lautenschlager & Wagner 1999; Halaj, Ross & Moldenke 2000; Liow, Sodhi & Elmqvist 2001; Sullivan, Sullivan & Lindgren 2001; Thompson, Baker & Ter-Mikaelian 2003), chiefly bird communities (Sekercioglu 2002; Hayes, Weikel & Huso 2003; Hagar, Howlin & Ganio 2004). These studies have found that the responses of bird communities to vegetation thinning are generally complex (Carey 2003), and positive effects on species richness and abundance of some species and an absence of species extirpation from thinned stands are usually described. However, the effects of thinning of the Mediterranean maquis on bird communities have not been previously addressed, although Sánchez-Zapata & Calvo (1999) have pointed out that habitat mosaics created by forestry and traditional farming are especially important for Mediterranean raptors.

Our major objective was to ascertain the effects of thinning the Mediterranean maquis on species richness, composition, abundance and conservation status of bird communities. We considered functional guilds of species according to their habitat use and trophic preferences by designing a large-scale 'natural experiment' that included paired thinned and unthinned maquis stands in central Spain. We also examined whether the effects of thinning demonstrated previously in other forest environments could be extended to the Mediterranean region. Further, we asked whether these effects depend upon the biogeographical origin and habitat requirements of its avifauna (Suárez-Seoane, Osborne & Baudry 2002). Finally, the experimental manipulation of vegetation by thinning allowed us to test the prediction of the macro-ecological hypothesis previously examined in a phylogenetic context (Polo & Carrascal 1999; Gaston & Blackburn 2000): the structural complexity and vegetation density of the habitat should act as a selective filter of the species' body masses, favouring settlement by small-sized species in complex and dense habitats because of manoeuvrability constraints.

Materials and methods

STUDY AREA

Field work was conducted in 21 maquis stands in Ciudad Real province located in the southern Spanish plateau. The study area is 19 749 km2 in extent and mid-coordinates are 38·9° north and 3·8° west. The altitude ranges between 423 and 999 m. The climate is continental Mediterranean, with dry, hot summers and cold winters. Mean annual temperature and total annual precipitation are 13·7 °C and 510 mm, respectively. An increasing aridity gradient can be recognized from north-west to south-east, annual rainfall ranging between 700 and 300 mm. The potential vegetation of most stands is dominated by the evergreen holm oak *Quercus ilex* L. However, land use has transformed these vast evergreen woodlands into a mosaic of patches dominated by woodland remnants, shrubland (e.g. *Quercus coccifera* L., *Erica arborea* L., *Cistus ladanifer* L. and *Rosmarinus oficinalis* L.), pasture lands and cropland. There is a shortage of fruit trees and shrubs in the area.

BIRD CENSUS

We selected 21 localities distributed throughout the study area to reflect its environmental heterogeneity, chiefly the aridity gradient. Each locality included a pair of maquis stands (thinned and unthinned). A thinned stand had to be at least 12 ha to be sampled; they averaged 19·9 ± 12·4 ha in extent. In the selected thinned stands, thinning was practised between 2 and 10 years before this study (4·1 ± 2·1 years). Stands were thinned by their landowners to favour cattle grazing and hunting, to reduce the risk of fires and to sell firewood. As close as possible to the selected thinned stands, and always within a 3-km radius, we selected an unthinned maquis stand with similar physical features including orientation, slope and soil type. Thus, the unthinned stands acted as reference stands that resembled the features of the thinned stands prior to human intervention.

Every stand was sampled by means of five point counts separated 100 m from each other, with each count lasting 10 min. The first and fifth point count was placed at least 100 m away from the stand edge. In each point count we established a circular plot of 50-m radius (Bibby *et al*. 2000) where we noted the presence and abundance of every bird species (see Appendix S1 in the supplementary material). Point count was the best census method in this habitat because unthinned stands were very dense and difficult to traverse. Nearly all detections were auditory (singing males, alarm calls, etc.), so bird detection was not dependent on vegetation obstruction or visibility. This method does not provide absolutes densities, but relative abundances. Nevertheless, the small area covered by the plots (0·78 ha) and the relatively long time devoted to bird counts, maximized the detection probability of species and, thus, accurate estimation of densities (Shiu & Lee 2003). Additionally, a preliminary census of the bird community to evaluate sampling efficiency indicated that our conclusions were not biased by detectability problems. Species richness was assessed by considering all species contacted in the pooled sample of the five 10-min stations, in order to include scarce species that would not normally be detected.

Censuses started at sunrise and lasted for *c*. 4 h. Sampling was carried out during the winter (December and January) and the breeding season (May and the first fortnight of June) in two consecutive years (2002 and 2003). All samples were obtained on rainless and nearly windless days (wind speed < 3 m s^{-1}) to reduce detectability problems. All censuses were conducted by the same researcher.

VEGETATION STRUCTURE

The vegetation structure was characterized after bird censuses in 10-m radius plots that coincided with the centres of the bird point counts. Habitat structure for each stand was measured using the average of the five 10-m plots. All habitat measurements (Table 1) were carried out by the same observer in order to avoid interpersonal bias.

SPECIES' CHARACTERISTICS

Data on body size, winter diet and main foraging substrata were obtained from Perrins (1998). The body mass of each species was calculated by averaging the data for adults of both sexes of the subspecies that inhabited the study region. The average body mass of bird species in each census plots was calculated by means of weighted averages, using the species densities in each locality stand as weights. The assignation of each species to an ecological category was made according to gross descriptions pertaining to food habits and spatial niche. Birds were grouped into seed-eaters, insectivorous and frugivorous species when, respectively, seeds, arthropods and fruits were the main constituents of the winter diet. The diet during the breeding season was not considered because all the species inhabiting the study area consume mainly arthropods during this time of the year. The spatial niche of species was categorized in the following groups: ground searchers (those mainly foraging on the ground, in the herbaceous layer or among leaf litter) and foliage gleaners (those mainly foraging among the leaves, twigs or small branches of trees or shrubs).

Table 1. Measured variables and summary statistics that describe the structure of the vegetation in $n = 21$ localities, comparing thinned (THIN) vs. unthinned or reference (REF) maquis stands. Sample size is $n = 21$. Degrees of freedom for repeated measure ANOVAS are 1, 20

	Mean		SE			
	THIN	REF	THIN	REF	*F*	*P*
Cover of bare ground (%)	22·1	26·3	4·4	4·9	0·79	0·385
Cover of moss (%)	9·9	12·5	2·6	3·1	4·04	0·058
Cover of herbaceous plants (%)	42·7	24·0	7·2	6·3	11·20	0·003
Cover of shrubs less than 25 cm tall (%)	10·0	6·2	2·0	1·5	3·36	0·082
Cover of shrubs 25–50 cm tall (%)	10·4	5·3	2·0	1·0	7·00	0·015
Cover of shrubs 50–100 cm tall (%)	7·4	7·2	2·0	1·6	0·01	0·947
Cover of shrubs 100–150 cm tall (%)	4·9	7·3	2·3	2·0	4·70	0·042
Cover of shrubs more than 150 cm tall (%)	6·8	20·7	2·8	5·1	6·76	0·017
Average height of shrubs (cm)	58·3	93·2	7·0	9·6	10·20	0·005
Tree crown cover (%)	24·6	36·9	2·7	4·2	9·34	0·006
Average height of trees (m)	3·7	3·8	0·2	0·2	0·00	0·998
Number of trunks less than 5 cm d.b.h. (no. ha^{-1})	181·1	651·6	31·6	79·2	32·40	0·000
Number of trunks 5–10 cm d.b.h. (no. ha^{-1})	283·3	351·7	50·8	77·7	0·85	0·367
Number of trunks 10–20 cm d.b.h. (no. ha^{-1})	67·5	56·0	13·3	14·4	0·78	0·387
Number of trunks 20–30 cm d.b.h. (no. ha^{-1})	6·7	6·0	2·9	1·9	0·05	0·823
Number of trunks more than 30 cm d.b.h. (no. ha^{-1})	2·5	3·8	1·2	1·5	0·70	0·411

Other spatial niche groups were omitted because of their under-representation in the sample (e.g. trunk searchers, aerial foragers, avian and mammal predators). For some bird species these categories were inadequate because the birds foraged on several substrata. In those cases, the density of the species was assigned proportionally to each spatial niche group or diet category.

The European endangered status of each species was obtained from Tucker & Heath (1994) using the Species of European Conservation Concern (SPEC) scores. However, this index of conservation concern only refers to breeding populations and many of the sampled species do not have SPEC scores as they are not considered of conservation concern. Twenty-six species were included in the category SPEC 4 because their global populations are concentrated in Europe but they have a favourable conservation status. Fifteen species were assigned to the category SPEC 3, denoting those birds whose global populations are not endangered but have an unfavourable conservation status in Europe. Eight species were considered of conservation concern because their populations were concentrated in Europe and have an unfavourable conservation status (SPEC 2). SPEC categories were scored as follows: non-SPEC, 5; SPEC 4, 4; SPEC 3, 3; SPEC 2, 2. The most abundant species within this last category in the studied stands were the red-legged partridge *Alectoris rufa* L., green woodpecker *Picus viridis* L., woodlark *Lullula arborea* L., black-eared wheatear *Oenanthe hispanica* L., Dartford warbler *Sylvia undata* Boddaert and woodchat shrike *Lanius senator* L. The average values of European conservation status (SPEC score) were calculated by means of weighted averages, using the species' densities in each locality stand as weights.

The influence of maquis thinning on gamebirds was analysed for those species of hunting interest: red-legged partridge *Alectoris rufa*, quail *Coturnix coturnix* L., woodpigeon *Columba palumbus* L., turtle dove *Streptopelia turtur* L., song thrush *Turdus philomelos* Brehm and mistle thrush *Turdus viscivorus* L. These species are hunted only in the winter season.

Data analysis

Data analyses were carried out by means of repeated-measures ANOVAS because of the paired design of our natural experiment. Two factors were included in the analyses: (i) thinned vs. unthinned treatments and (ii) seasonal differences (winter vs. spring censuses). The interaction term thinning × season was also included in the two-way ANOVAS to test if the effects of thinning were persistent across seasons. One-way repeated-measures ANOVAS were only possible in one season for winter trophic groups, winter density of gamebirds and the SPEC scores for breeding populations. All statistical tests used the means per stand as the sample unit (i.e. the average of census samples per year in two consecutive years).

The time elapsed between the years when thinning was practised and the years when birds were censused were not homogeneous in the 21 study localities (see above). The influence of this effect on thinning was tested by means of the partial correlation between the measures of vegetation structure in thinned stands and the time elapsed, controlling for the effect of the measures in unthinned stands. None of the partial correlations for the 16 habitat variables was significant ($P > 0{\cdot}107$). Therefore, the heterogeneity across the 21 localities in the time elapsed since thinning did not introduce any bias in the comparisons of thinned vs. unthinned stands. All statistical analyses were carried out using STATISTICA 6·0 (StatSoft 2001).

Results

Effects of thinning on vegetation structure

Thinning reduced the cover of shrubs taller than 100 cm, average height of shrubs, cover of trees and number of trunks less than 5 cm d.b.h. (Table 1). Conversely, it increased the cover of herbaceous vegetation and shrubs shorter than 50 cm.

Effects of thinning on bird community

Considering both study seasons together, 11 common (> 1 bird 10 ha^{-1}) species were at least 33% more abundant in thinned stands than in unthinned maquis: corn bunting *Miliaria calandra* L., woodchat shrike, thekla lark *Galerida theklae* Brehm and bee-eater *Merops apiaster* L. in spring; and chaffinch *Fringilla coelebs* L., woodpigeon, woodlark, magpie *Pica pica* L., azure-winged magpie *Cyanopica cooki*, mistle thrush and spotless starling *Sturnus unicolor* Temminck in winter. Conversely, only six common species were more abundant (> 33%) in unthinned maquis than in thinned stands: Sardinian warbler *Sylvia melanocephala* Gmelin, long-tailed tit *Aegithalos caudatus* L. and blackbird *Turdus merula* L. in both seasons; linnet *Carduelis cannabina* L. in spring; and Dartford warbler and firecrest *Regulus ignicapilla* Temminck in winter.

Thinning was responsible for a significant increase in species richness but did not have any effect on bird density. Species richness and bird density significantly changed between seasons, richness being higher in spring than in winter, and density being higher in winter than in spring (Fig. 1 and Table 2a). The interaction term season × thinning was never significant; thus, the effects of thinning were consistent and homogeneous across seasons.

Average body mass of bird species in thinned stands was significantly larger than in unthinned maquis, and in spring than in winter (Fig. 2 and Table 2a). The interaction term season × thinning was not significant; thus, the effect of thinning on average body mass of bird was consistent and homogeneous across seasons.

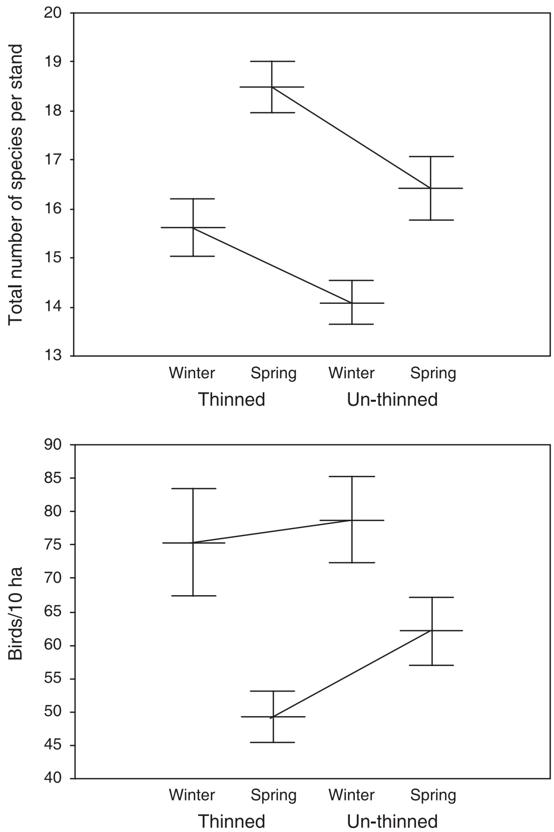

Fig. 1. Variation in total bird species richness (upper part) and average density (lower part) in thinned and unthinned (reference) stands across two study seasons. Bars represent mean ± 1 SE. The census plots cover an area of 0·78 ha (i.e. circular plots of 50-m radius). Sample size is 21 stands.

EFFECTS OF THINNING ON GUILDS

Density of ground searchers was indistinguishable in thinned and in unthinned stands, whereas density of foliage gleaners was higher in unthinned than in thinned stands. These two foraging guilds were denser in winter than in spring (Tables 2b and 3a). These patterns were consistent across seasons and thinning treatments (the interaction term thinning × season was not significant).

Winter density of granivorous species was marginally higher in thinned stands, whereas insectivorous and frugivorous species were marginally more abundant in unthinned maquis (Tables 2b and 3a).

EFFECTS OF THINNING ON CONSERVATION STATUS AND DENSITY OF GAMEBIRDS

The average SPEC score of the bird species was significantly different in thinned than unthinned stands during the breeding season (Tables 2c and 3b). Thinned areas supported greater densities of bird species of high conservation concern.

Winter density of gamebirds was significantly affected by thinning, being higher in thinned than unthinned stands (Tables 2d and 3c).

Discussion

THINNING AND VEGETATION STRUCTURE

Thinning eliminates the understorey woody vegetation to reduce competition for the biggest oaks, resulting in a more open woodland that favours the growth of the herbaceous layer. It has the potential to increase the structural diversity of unmanaged monotonous stands, promoting the development of habitat attributes characteristic of later serial habitats (Hagar, Howlin & Ganio 2004). Our data indicate that, on average 4 years after thinning, the herbaceous, short shrub and tree cover increased by 50–100%. These changes were the result of increased light availability, regrowth and reduced intra- and interindividual competition between trees (Perevolotsky & Haimov 1992; Haveri & Carey 2000;

Table 2. Results of the repeated-measures ANOVA testing for the effects of thinning and seasonal differences (winter vs. spring) in census plots. In the analyses of guilds, the effect of thinning on winter densities of birds is tested using the sample of winter censuses (i.e. no estimation of the effects of season and interaction terms). The analysis of endangered status is performed with data during the breeding season, because SPEC scores refer to European breeding populations. Degrees of freedom are 1, 20 for all tests

	Thinning		Season		Interaction	
	F	*P*	*F*	*P*	*F*	*P*
(a) Community variables						
Species richness	11·93	0·002	16·18	< 0·001	0·37	0·550
Total density	2·65	0·119	16·14	< 0·001	1·52	0·232
Average body mass	5·26	0·033	13·76	0·001	0·11	0·748
(b) Foraging guilds						
Density of ground searchers	1·44	0·244	7·64	0·012	2·25	0·149
Density of foliage gleaners	10·14	0·005	20·44	< 0·001	0·05	0·829
Winter density of granivorous birds	3·12	0·092				
Winter density of insectivorous birds	3·93	0·061				
Winter density of frugivorous birds	3·64	0·071				
(c) European endangered status	5·03	0·036				
(d) Winter density of gamebirds	4·33	0·050				

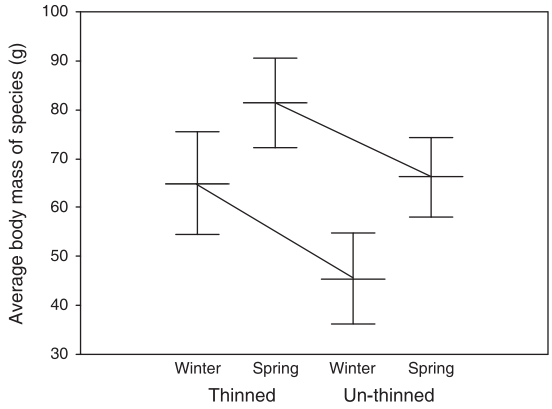

Fig. 2. Variation in average body mass of bird species in thinned and unthinned (reference) stands across two study seasons. Bars represent mean ± 1 SE. Sample size is 21 stands. The average body mass of bird species in each census plots was calculated by means of weighted averages, using the species' densities in each locality stand as weights.

Artman 2003). On the other hand, the cover of tall shrubs (> 100 cm) and saplings (< 5 cm d.b.h.) was reduced by 100–200% (Table 1). We estimate that in *c*. 12 years, under similar climate conditions, the thinned stands would attain the previous vegetation density. This represents a relatively rapid recovery of vegetation after disturbance. Consequently, thinned stands need to be maintained through further periodic thinning or grazing by cattle; other natural disturbances such as fire would also maintain open stands (Perevolotsky & Haimov 1992; Kaplan & Gutman 1996; Sekercioglu 2002; Brotons *et al*. 2003; Brotons, Herrando & Martin 2004).

THINNING AND BIRD COMMUNITIES

Thinning was responsible for a significant increase in bird species richness. The homogeneous habitat structure of the natural maquis in the study area supports a poor bird community dominated by a low number of common species such as the sardinian warbler, long-tailed tit, Dartford warbler, chaffinch, great tit and blue tit. The structural diversity of thinned stands creates habitats suitable for several bird species that are scarce in dense maquis (e.g. corn bunting, woodchat shrike, thekla lark, bee-eater, woodlark, magpie, azure-winged magpie, mistle thrush, woodpigeon and spotless starling). In contrast, thinning decreased the density of several previously dominant species (e.g. Sardinian warbler, Dartford warbler, long-tailed tit and firecrest) but no species were lost from stands following this practice. These results are consistent with those obtained from other studies of bird responses to thinning in different regions across the northern hemisphere (Haveri & Carey 2000; Artman 2003; Thompson, Baker & Ter-Mikaelian 2003; Hagar, Howlin & Ganio 2004). The higher species richness in thinned stands could be explained by the intermediate disturbance hypothesis, which predicts a peak of diversity under a moderate removal of biomass compared with undisturbed natural habitats (Solonen 1996; Wilkinson 1999). In our study, alteration of the homogeneous structure of maquis by thinning led to an increase in habitat heterogeneity, which is the main factor responsible for diversity in bird communities (see Wiens 1989 and references therein). The effects of thinning on Mediterranean bird communities appear to mirror those induced by other disturbances such as fire (Herrando, Brotons & Llacuna 2003; Brotons, Herrando & Martin 2004). Habitat heterogeneity at a local scale seems to be a key factor in maintaining bird diversity in disturbed Mediterranean landscapes. In particular, open-space species respond positively to changes in habitat structure, leading to increased local abundance. Thus, it appears that changes in the structure of vegetation as a result of different ecological disturbances, such as fire and thinning, may promote similar changes on these bird communities.

Table 3. Mean and SE of variables describing the bird communities in paired thinned and unthinned (reference) stands during the winter and breeding (spring) seasons. $n = 21$ localities. Figures for densities are averages in five 50-m radius plots (i.e. birds 0·78 ha^{-1})

		Thinned		Reference	
		Winter	Spring	Winter	Spring
(a) Foraging guilds					
Density of ground searchers	Mean	2·60	1·58	2·14	1·62
	SE	0·34	0·18	0·26	0·21
Density of foliage gleaners	Mean	3·25	1·94	4·01	2·83
	SE	0·39	0·20	0·45	0·26
Winter density of granivorous birds	Mean	1·56	–	0·97	–
	SE	0·36	–	0·14	–
Winter density of insectivorous birds	Mean	3·73	–	4·51	–
	SE	0·37	–	0·46	–
Winter density of frugivorous birds	Mean	0·47	–	0·70	–
	SE	0·12	–	0·17	–
(b) European endangered status in spring	Mean	–	3·80	–	3·96
	SE	–	0·07	–	0·10
(c) Winter density of gamebirds	Mean	0·82	–	0·48	–
	SE	0·21	–	0·12	–

The significance of the effects on the birds of this region was generally low, in spite of the marked changes in habitat structure introduced by maquis thinning. This contrasts with the observed patterns in other woodland environments of northern latitudes but may be explained, at least partially, by considering the biogeographical basis of the avifauna in the Mediterranean region. Mediterranean bird species are restricted to the early stages of succession and are then replaced by temperate forest species (Preiss, Martin & Debussche 1997). Xeric woodland environments of this region support an impoverished European forestal avifauna (Mönkkönen 1994; Covas & Blondel 1998). Density and species richness decrease towards the south of the Iberian Peninsula, and follow a pattern that is inversely related to rainfall and directly associated with temperature (Tellería & Santos 1993), the main determinants of primary productivity in dry Mediterranean environments (Mooney & Kummerow 1981). Only generalist woodland species (such as the chaffinch and the great tit) and those species that are common in the Mediterranean basin inhabit these woodland stands (e.g. Dartford and black-headed warblers). Therefore, the low impact of thinning on the avifauna of the study region can be attributed to the small regional pool of species typical of well-developed woodlands, and the fact that the dominant bird species in this region are those mainly associated with shrublands and evergreen forests of low tree height (Suárez-Seoane, Osborne & Baudry 2002).

A dense undergrowth of shrubs and young trees inhibits the development of a complex shrub and herbaceous strata, which therefore limits the feeding opportunities for ground and shrub gleaners (for similar results in other forest types see Haveri & Carey 2000; Hayes, Weikel & Huso 2003; Hagar, Howlin & Ganio 2004). The elimination of this dense understorey through thinning operations would be expected to increase the abundance of these functional guilds and limit the abundance of foliage gleaners and insectivorous birds. Both predictions are supported by our results, which have been also reported in other forest environments (Easton & Martin 1998).

THINNING AND BODY SIZE OF BIRD SPECIES

Slender and pliable substrata, such as foliage and thin twigs, are mainly exploited by small-sized birds because of ecomorphological constraints on manoeuvrability (Miles & Ricklefs 1984; Suhonen, Alatalo & Gustafsson 1994). Accordingly, the average body mass of bird assemblages is related to habitat structure and the use of foraging substrata (Gunnarsson 1992; Dixon, Kin-dlmann & Jarosik 1995; Polo & Carrascal 1999). Bird species that thrive in densely vegetated habitats and forage on foliage are lighter than those living in open habitats that forage on the ground (Polo & Carrascal 1999). Our results are in agreement with these patterns, as the average body mass of species in thinned stands was significantly higher than in unthinned maquis. To our knowledge, this is the first time that a large-scale experimental manipulation of habitat structure and vegetation volume has demonstrated the predicted allometric effect of habitat structural complexity on the average body mass of a bird community. This relationship had been previously observed from comparisons of several species differing in body mass and habitat preferences. Nevertheless, these traits have a remarkable phylogenetic correlation (Polo & Carrascal 1999; Freckleton, Harvey & Pagel 2002) so the relationship between them may emerge as a consequence of the evolutionary history of the group. In ecological time, the results of our study can be explained if we assume that structural complexity and vegetation density act as a selective filter of the bird fauna of the region, allowing the establishment and promoting the increase of density of small-sized species in the densely vegetated, unthinned maquis. The higher average body mass in thinned stands is a consequence of both the increased density of relatively large species that mainly forage on the ground and the decreased density of relatively small species that usually forage on the foliage and twigs affected by thinning.

IMPLICATIONS FOR SPECIES CONSERVATION AND HUNTING

We found that thinned stands supported bird species of high conservation concern in Europe. We did not record any species threatened with extinction (SPEC 1). Species such as red-legged partridge, woodchat shrike and wood lark, with SPEC 2, tended to be more abundant in thinned than unthinned stands, making this habitat important for species conservation. These results have to be considered cautiously because these species are actually rather common at the regional level. Nevertheless, we point out that thinning did not adversely affect the local abundance of endangered species in our study. As thinned and unthinned stands favoured different guilds, management directed toward a single species or species group and extensive, conventional forestry are unlikely to be successful for the conservation of bird communities that inhabit complex forest ecosystems (Artman 2003; Carey 2003; Thompson, Baker & Ter-Mikaelian 2003; Hagar, Howlin & Ganio 2004). Both thinned and unthinned areas should be maintained.

Hunting is an important economic activity in the region, and provides more monetary value per area unit than, for example, agriculture. The value of forest management for hunting has been reported for several game species (Terry, McLellan & Watts 2000). The winter abundance of gamebirds increased in thinned stands because these birds are mostly granivorous and frugivorous species that prefer to forage in this habitat rather than in dense maquis (for wintering birds in central Spain see Carrascal, Palomino & Lobo 2002). However, they rely on more dense vegetation patches (red-legged

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partridge) and trees (wood pigeon, turtle dove, song thrush and mistle thrush) for nesting. Thus, a habitat mosaic of dense and open woody vegetation (Scarascia-Mugnozza *et al*. 2000) is necessary for the maintenance of populations of valuable gamebirds.

In conclusion, our results indicate that thinning of the Mediterranean maquis modifies the structure of the vegetation and, as a consequence, also alters several aspects of bird community structure, including species richness, guild composition and average body mass. The effects were consistent across seasons except for body mass. Thinning of dense Mediterranean woodlands dominated by shrubs and young trees enhances habitat suitability for several species of birds, but some unthinned patches should be preserved to provide refugia for species that are impacted by thinning (Hayes, Weikel & Huso 2003; Hagar, Howlin & Ganio 2004). Silvicultural thinning was also found to be beneficial for threatened bird species in the European context and for gamebirds, emphasizing both its conservation and economic values.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1. Densities (birds 10 ha^{-1}) of bird species in thinned and unthinned stands of the study area, Ciudad Real, central Spain.

Appendix

Common name	Species	Thinned stands winter	Thinned stands spring	Control maquis winter	Control maquis spring
Long-tailed tit	*Aegithalus caudatus* (5,I,f)	5.43	2.20	12.76	7.51
Red-legged partridge	*Alectoris rufa* (2,G,g,H)	2.93	2.20	3.11	1.77
Buzzard	*Buteo buteo* (5,C,g)	0.06	0.06	---	---
Linnet	*Carduelis cannabina* (4,G,g)	0.37	0.24	0.12	1.89
Goldfinch	*Carduelis carduelis* (5,G,g)	0.43	0.31	0.37	0.55
Greenfinch	*Carduelis chloris* (4,G,g)	---	0.12	---	0.37
Siskin	*Carduelis spinus* (4,G,f)	0.24	---	---	---
Short-toed treecreeper	*Certhia brachydactyla* (4,I,t)	---	0.12	0.37	0.37
Great spotted cuckoo	*Clamator glandarius* (5,g)	---	0.37	---	0.31
Woodpigeon	*Columba palumbus* (4,G,g,H)	2.08	2.32	0.73	2.20
Quail	*Coturnix coturnix* (3,g,H)	---	0.12	---	---
Cuckoo	*Cuculus canorus* (5,g)	---	0.12	---	0.06
Azure-winged magpie	*Cyanopica cyana* (4,I,g)	1.59	3.11	0.31	2.50
Rock bunting	*Emberiza cia* (3,G,g)	0.31	0.24	0.43	0.12
Cirl bunting	*Emberiza cirlus* (4,G,g)	---	---	---	0.12
Robin	*Erithacus rubecula* (4,I,g)	12.51	0.12	14.71	---
Chaffinch	*Fringilla coelebs* (4,G,f)	9.46	5.43	5.49	4.88
Thekla lark	*Galerida theklae* (3,G,g)	0.31	1.59	0.55	0.98
Jay	*Garrulus glandarius* (5,G,g/f)	---	0.31	---	0.24
Melodious warbler	*Hippolais polyglotta* (4,f)	---	0.06	---	0.12
Swallow	*Hirundo rustica* (3,a)	---	0.85	---	0.24
Great grey shrike	*Lanius meridionalis* (3,I,g)	---	0.31	---	---
Woodchat shrike	*Lanius senator* (2,g)	---	1.53	---	0.49
Wood lark	*Lullula arborea* (2,G,g)	1.65	0.49	0.49	0.18
Bee-eater	*Merops apiaster* (3,a)	---	2.50	---	1.22
Corn bunting	*Miliaria calandra* (4,G,g)	---	1.40	0.31	0.37
Spotted flycatcher	*Muscicapa striata* (3,a)	---	---	---	0.31
Blue tit	*Parus caeruleus* (4,I,f)	4.09	2.32	5.25	2.93
Crested tit	*Parus cristatus* (4,I,f)	0.18	0.24	0.31	0.06
Great tit	*Parus major* (5,I,f)	4.70	3.24	5.37	3.11
Spanish sparrow	*Passer hispaniolensis* (5,G,g)	---	0.43	---	0.12
Tree sparrow	*Passer montanus* (5,G,g)	---	---	---	0.18
Black redstart	*Phoenicurus ochruros* (5,I,g)	0.24	---	---	---
Bonelli’s warbler	*Phylloscopus bonelli* (4,f)	0.18	0.43	---	0.43
Chiffchaff	*Phylloscopus collybita* (5,I,f)	4.94	---	5.19	---
Magpie	*Pica pica* (5,C,g)	1.59	0.18	0.06	0.73
Greenn woodpecker	*Picus viridis* (2,I,g/t)	0.06	0.06	0.06	0.24
Dunnock	*Prunella modularis* (4,G,g)	0.49	---	0.49	0.06
Crag martin	*Ptyonoprogne rupestris* (5,I,a)	0.92	0.31	---	0.92
Firecrest	*Regulus ignicapillus* (4,I,f)	2.26	0.37	4.46	---
Serin	*Serinus serinus* (4,G,g)	0.49	1.65	0.37	2.14
Turtle dove	*Streptopelia turtur* (3,g,H)	---	0.12	---	0.43
Spotless starling	*Sturnus unicolor* (4,G,g)	1.22	---	---	0.24
Blackcap	*Sylvia atricapilla* (4,F,f)	0.06	0.18	---	0.18
Subalpine warbler	*Sylvia cantillans* (4,f)	0.18	0.73	---	1.04
Orphean warbler	*Sylvia hortensis* (3,f)	---	0.18	---	0.06
Sardinian warbler	*Sylvia melanocephala* (4,F,f)	2.99	5.92	5.49	10.13
Dartford warbler	*Sylvia undata* (2,I,f)	6.90	3.36	7.14	5.68
Blackbird	*Turdus merula* (5,F,g)	1.40	2.26	3.11	3.97
Song thrush	*Turdus philomelos* (4,I,g)	3.97	---	1.89	---
Mistle thrush	*Turdus viscivorus* (4,F,g)	1.59	0.37	0.37	0.55
Hoopoe	*Upupa epops* (5,I,g)	0.06	0.24	---	0.12
Total density		75.88	48.72	79.30	60.13
Number of species		34	43	27	43
Diversity (Shannon index)		2.87	3.13	2.59	2.96

Appendix: Densities (birds/10 ha) of species in the thinned and un-thinned stands of the study area in Ciudad Real (Central Spain). One hundred and five circular census plots (50 m in radius) were surveyed in 21 localities in both thinned and control stands. Each census plot was repeated two times per year, in two consecutive years (i.e., four replicates per census plot). ---: species absent.

SPEC scores define the European conservation status: 5 (non-endangered category), 4, 3, 2 (the most endangered category).

Winter foraging guilds: carnivorous (C), granivorous (G), insectivorous (I), frugivorous (F).

Main foraging substrata: aerial feeder (a), foliage gleaners (f), ground searchers (g), trunk foragers (t).

Game species (H).

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