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Habitat disturbance in Mediterranean landscapes: Effects of fire and fragmentation on birds

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Als meus pares...

....per haver-me donat la vida i una manera de veure-la.

És evident que considerar un fet com bona o mala sort depèn de la manera de veure-ho de cadascú. Tanmateix, els més independents de les circumstàncies externes tindran menys tendència a classificar les coses com bones o dolentes.

Lie Tse, segle IV a.C.

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HABITAT DISTURBANCE IN MEDITERRANEAN LANDSCAPES: EFFECTS OF FIRE AND FRAGMENTATION ON BIRDS

INTRODUCTION

Much of the early development of ecology was premised on the comfortable notion that population dynamics were in a state of equilibrium. More recently, theoretical and empirical interest has shift away from this deterministic perspective to place much more emphasis on the role of disturbances on natural systems (Meffe et al 1997). Pickett & White (1985) defined disturbances as relatively discrete events in time that disrupt the structure of ecosystems. Sooner or later all natural systems are affected by some form of disturbance, which contributes to the spatial and temporal dynamics of species and communities (Turner 1987). In contrast with former tendencies, which were centred on the process of re-organisation known as succession (Odum 1969), current thought often emphasises the dynamics of disturbed patches in both space and time (Forman 1995, Meffe et al 1997). This perspective allows a better approximation to highly dynamic landscapes such as those of the Mediterranean Basin, where temporal and spatial patterns related to disturbances are probably closer to a rule than an exception.

Due to the transitional position between cold temperate, and dry tropical climates, the Mediterranean climate is especially variable and unpredictable. Consequently, Mediterranean landscapes are periodically affected by natural disturbances associated with extreme weather conditions such as flooding, drought, severe cold spells and wildfires, which, together with the diverse topography, geology and geography, configure their heterogeneous mosaics (Blondel & Aronson 1999). Among these disturbances, fire deserves special attention since it is considered one of the major forces that influences the ecosystems of the region (Trabaud 1981). Furthermore, fires not only affect burnt ecosystems themselves but also strongly modify previous landscape patterns, causing the appearance of new landscape units, the elimination of others and the fragmentation of remnant patches (Trabaud & Galtié 1996).

Human activity is another key factor to consider in understanding the spatial and temporal dynamics of natural systems in the Mediterranean Basin. Like few other regions in the world, humans have shaped the Mediterranean landscapes for millennia by means of practices such as burning, cutting, cultivating, terracing, hunting, livestock breeding or irrigating (Trabaud 1981, Blondel & Aronson 1999). With few exceptions, this long-lasting management of the Mediterranean has not resulted in a sharp decrease in biodiversity. On the contrary, it appears that, in general, the continuous redesign of fragmented Mediterranean landscapes with frequent but moderate disturbances has been beneficial for many organisms (Farina 1997, Blondel & Aronson 1999).

Nevertheless, during the 20th century, Euro-Mediterranean countries have undergone the homogenisation of the formerly fine-grained land mosaics. On one hand, the abandonment of traditional land use in mountain regions because of marginal profits has led to the spread of woodland and shrubland (Preiss et al. 1997). Fuel accumulation has contributed to increasing wildfire hazards and, consequently, has had a relevant role in the increase of the total burnt area (Le Houerou 1990). Moreover, the progressive deterioration of climate during the second half of the century, characterised by drier and warmer conditions, has also contributed to increasing areas affected by fire (Piñol et al. 1998). On the other hand, human activity has intensified in fertile valleys and along coasts, where natural vegetation patches have become progressively more scarce and isolated. Available data suggests that both extremes, the abandonment and the intensification of land use leads to decreased biological diversity (Blondel & Aronson 1999).

Ecological research in this complex framework did not start until recently and little is known about the response of organisms to both traditional and recent disturbance regimes, which involve such distinct landscape patterns. This is, therefore, a challenge for researchers, who should not only attempt to understand the role of disturbances on wildlife but also provide feasible guidelines for compatible land management and biological conservation.

Birds have been widely used to monitor habitat and landscape alterations because they are relatively easy to monitor and are reliable and known biological indicators (Furness & Greenwood 1993). Furthermore, many Mediterranean bird species are classified as vulnerable or endangered (Tucker & Heath 1994) and hence, the environmental factors that affect these species are receiving special attention from investigators and wildlife managers alike. Within this framework, this thesis attempts to contribute to the knowledge of the relationships between birds and disturbances in Mediterranean landscapes; specifically, it focuses on the effects of fire and fragmentation on bird communities.

Fire and Mediterranean birds

Despite the high frequency of fires in Mediterranean landscapes, few studies have been carried out on their effects on bird populations (Prodon & Pons 1993). However, the last two decades have brought valuable data, especially from studies carried out in southern France by R. Prodon and others.

Due to their ability to fly, birds can often avoid the direct effects of flames through moving into adjacent habitats not affected by the passage of fire (Lawrence 1966). Nevertheless, the drastic modification of habitat has important consequences on the re-colonisation of the burnt area. Due to their strong philopatry, habitat tolerance, and to the persistence of standing dead trees, some species can return to burnt territories the first breeding season after fire, but they progressively leave their breeding territories and do not reappear until the vegetation attains a woody appearance (Prodon et al. 1987, Pons & Prodon 1996). Apart from these exceptional cases, the post-fire succession of bird communities is closely linked with vegetation recovery, first starting with open-space species, then shrubland species and finally forest species (Prodon et al. 1984). Within this context, and from a conservational perspective, it should be noted that in Mediterranean environments the initial successional stages provide suitable habitats for many vulnerable bird species (Rocamora 1997). In contrast, woodland bird communities are essentially composed of species that are widespread and common in the Western Palaearctic (Blondel & Farré 1988).

The intervention of man in the successional process has also been studied in relation to the extraction of burnt timber, which causes appreciable deviations from the spontaneous turnover of bird communities after fire (Llimona et al. 1993, Izhaki & Adar 1997). Finally, regarding the increasing interest in the use of prescribed burning to prevent large fires (Miller & Hardy 2000), Pons (1998) studied the effects of these small fires and showed that the enhancement of habitat heterogeneity allowed the persistence of all species that inhabited the zone before the burning, and even allowed the recruitment of some open-space passerines.

To date, most studies on the effects of fire on birds in the Mediterranean Basin have been carried out in the mesic “meso-Mediterranean” life-zone (see box 2) (e.g. Prodon et al. 1984, Prodon et al. 1987, Vicente 1991, Pons & Prodon 1996, García 1997) and data from the drier and warmer “thermo-Mediterranean” life-zone, which is even more affected by fires, are scarce. Within this geographical context, this thesis analyses some temporal and spatial patterns of bird communities related to the occurrence of fire.

Fragmentation and birds in Mediterranean landscapes

The study of the effects of habitat fragmentation on birds in Mediterranean landscapes also remained poorly developed until recently. Over the last 10 years, a group of researchers from the Universidad Complutense de Madrid headed by J.L. Tellería and T. Santos have obtained a considerable amount of data on forest fragments in the Iberian Plateaux.

As shown in other temperate regions of the world (e.g. Hinsley et al. 1995, Bellamy et al. 1996), Díaz et al. (1998) found that fragment size was the major factor behind the patterns of bird occupancy in Iberian forest patches. Studying the effects of fragmentation in areas with low total forest cover, these authors also showed that birds were negatively influenced by the isolation of remnant patches. This result was consistent with that reported by Andrén (1994), who suggested that this effect appeared in landscapes that contain less than 30% of suitable habitat. However, as suggested by Mönkönen and Reunanen (1999), this pattern cannot be generalised because in another study in landscapes with less than 20% of forest cover, Tellería & Santos (1999) did not observe any significant effect of isolation. Another interesting result is that of the effect of ecological densities on the ability of birds to occupy fragments, the most abundant species being those tending to occupy a wider range of forest sizes and the more scarce species those which tend to reside only in larger forests (Díaz et al. 1998, Tellería & Santos 1999). Finally, Tellería & Santos (1997) found that the between-year persistence in the occupation of fragments was directly related to species abundance.

Therefore, these data suggest that, in spite of the particular history of forest fragmentation in the Mediterranean Basin, forest species respond to this disturbance in a similar way as in other regions. Nevertheless, to date, most studies have focused on forest archipelagos located within cereal cropland matrixes on the Iberian Plateaux and no data are available from shrubby matrixes, which are common in many coastal regions of the Mediterranean Basin. Given the importance of matrix type for birds inhabiting remnant isolates (Pearson 1993, McGarigal & McComb 1995, Sisk et al. 1997, Saab 1999), I studied forest fragmentation within shrubby matrixes (both agricultural and natural) of the Northeast Iberian Peninsula. Moreover, this thesis has also focussed on the little studied effects of fragmentation in Aleppo pine forests, which constitute one of the most common forest types in fragmented landscapes that surround the Mediterranean Sea.

Box 1: Bird species

This thesis is about the overall bird community, except raptors and aerial feeders such as swallows and swifts. Richness, abundance and ecological ordinations of species have been widely used as bird community descriptors to test several predictions. However, specific population responses have been considered when appropriate for testing the hypothesis (Chapter 3 and Chapter 6). Most of the fieldwork was carried out during the breeding season but some was also done in the wintering season. No attempt has been made to monitor relationships between habitat disturbances and long-distance migrants because these birds only reside the Mediterranean area for brief periods in autumn and spring. Although they may also be highly influenced by disturbances, their short stay in the area and their high mobility make it extremely difficult to study the response of such species to disturbances.

Box 2: Study area
Most of the previous research about the effects of disturbances on Mediterranean birds has been carried out in the meso-Mediterranean life-zone, which is characterised by Holm-oak forests (Blondel & Aronson 1999). This contrasts with the scarcity of data from the warmer and drier thermo-Mediterranean life-zone, characterised by dense coastal shrublands (nowadays heavily degraded) of wild olive tree, carob tree, lentisk or Mediterranean dwarf palm This thesis is essentially focused on the second life-zone but in the fragmentation studies partly penetrated the meso-Mediterranean zone. Field work was carried out in the calcareous mountain ranges and valleys of the coast of the Northeast Iberian Peninsula, between the cities of Barcelona and Tortosa. Specifically, most of field work (five chapters) was done exclusively in the Garraf Natural Park.

Objectives of the thesis

The main objective of this thesis is to analyse how fire and fragmentation in Mediterranean habitats affect birds. Each chapter of this work poses questions and hypothesises about the ecological responses of birds to these disturbances. At present, the relationship between avian communities and habitat changes is one of the main areas of interest with respect to bird conservation (Tucker & Evans 1997). Therefore, whenever findings are considered relevant for conservation, special attention has been taken to show the contributions of this research to wildlife management. The specific objectives of this thesis can be explained as follows.

The first objective was to analyse the succession of bird communities after fire in a “thermo-Mediterranean” zone. I carried out this research in the Garraf Natural Park and, given that the dryness of the zone may provoke slow vegetation recovery, I hypothesised that bird succession would also be characterised by a slow recovery of richness and abundance and, at the same time, by a slow change from communities dominated by open-space bird species to those dominated by shrubland birds (Chapter 2). Furthermore, I focussed on two species (the Dartford Warbler *Sylvia undata* and the Sardinian Warbler *Sylvia melanocephala*) to analyse whether post-fire dynamics could be influenced by population trends on a larger scale than that of the disturbed habitat (Chapter 3).

Large wildfires cause a loss of landscape heterogeneity by converting the vegetal mosaic into a homogeneous burnt area. In Chapter 4, I study the spatial variability of bird communities in zones affected by fires to a variable degree. Specifically, I address two main questions: Are bird communities more spatially uniform in burnt than in unburnt areas? Do the species that inhabit burnt and unburnt zones respond similarly to changes in habitat structure?

It is generally accepted that mature systems contain a more stable bird community than disturbed ones. Therefore I hypothesised that bird communities in burnt zones undergo greater seasonal changes than those in unburnt areas. Field censuses of breeding and wintering birds in three zones of the Garraf Natural Park were carried out to test this hypothesis (Chapter 5).

The study of the effects of habitat changes on birds has generally been based on the conception that bird abundance is a reliable indicator of population responses to habitat transformation. Nevertheless, abundance estimates do not provide direct information about the quality of individuals in a given habitat (Van Horne 1983, Wiens 1989). For this reason, I conducted a study to determine whether the individuals of a species capable of inhabiting both burnt and unburnt areas (the Sardinian Warbler *Sylvia melanocephala*) showed differences in their body condition in these two areas. This research was made using measures of tail feather asymmetry from Sardinian Warblers (Chapter 6).

As explained above, wildfires play a major role in fragmenting Mediterranean forests. Chapter 7 of this thesis addresses, for first time, the consequences of fires on birds inhabiting forest patches that remain unburnt after the passage of fire. Considering the historical role of this disturbance on Mediterranean landscapes, I hypothesised a moderate impact of this type of fragmentation on these species.

Finally, the last chapter of this thesis analyses the factors that determine bird assemblages in fragments of Aleppo pine forest surrounded by vineyards. Special attention is drawn to the effect of forest size, level of isolation, role of riparian corridors and vegetation composition and structure (Chapter 8).

PERTORBACIONS DE L'HÀBITAT EN PAISATGES MEDITERRANIS: EFECTES DEL FOC I DE LA FRAGMENTACIÓ EN OCELLS

INTRODUCCIÓ

Bona part del desenvolupament inicial de l'ecologia estava centrat en la confortable noció que les dinàmiques poblacionals estaven en un estat d'equilibri. Més recentment, l'interès teòric i empíric ha fugit d'aquesta perspectiva determinística i ha donat més importància al paper de les pertorbacions en els sistemes naturals (Meffe et al 1997). Pickett & White (1985) van definir les pertorbacions com esdeveniments discrets en el temps que desbaraten l'estructura de l'ecosistema. Tard o d'hora, tots els sistemes naturals són afectats per alguna de les múltiples formes de pertorbació, les quals contribueixen a la dinàmica espacial i temporal de les espècies i de les comunitats (Turner 1987). En contrast amb les primeres tendències, que estaven centrades en el procés de reorganització conegut com a successió (Odum 1969), el pensament actual sovint emfatitza la dinàmica de les unitats pertorbades en l'espai i el temps (Forman 1995, Meffe et al 1997). Aquesta perspectiva permet una millor aproximació a la realitat de paisatges altament dinàmics com els de la conca mediterrània, on els patrons temporals i espacials relacionats amb les pertorbacions estan probablement més a prop de la norma que de l'excepció.

Degut a la seva posició de trànsit entre els climes temperats freds i els tropicals secs, el clima mediterrani és especialment variable i impredictible. En conseqüència, els paisatges mediterranis estan periòdicament afectats per pertorbacions naturals associades a extrems meteorològics, com inundacions, sequeres, fredorades i focs, les quals, junt a una topografia, geologia i geografia diversa, configuren l'heterogeni mosaic dels paisatges mediterranis (Blondel & Aronson 1999). Dins d'aquest conjunt de pertorbacions, el foc mereix una consideració especial ja que representa una de les majors forces que influeixen el els ecosistemes de la regió (Trabaud 1981). A més, el foc no només afecta els ecosistemes incendiats sinó que modifica fortament els patrons de paisatge amb l'aparició de noves unitats paisatgístiques, l'eliminació d'altres i la fragmentació de les no directament cremades (Trabaud & Galtié 1996).

L'home és un altre factor clau per a la comprensió de la dinàmica temporal i espacial dels sistemes naturals de la conca mediterrània. Com a poques altres regions del món, els humans han modelat els paisatges del voltant de la mar mediterrània des de fa mil·lenis a través de pràctiques com els incendis, les tales, el conreu, la construcció de terrasses, la caça, l'alimentació del bestiar o la irrigació dels camps (Trabaud 1981, Blondel & Aronson 1999). Amb poques excepcions, aquesta ancestral gestió de l'espai no ha resultat en una marcada disminució de la biodiversitat. Al contrari, en conjunt, el continu redisseny dels fragmentats paisatges mediterranis, amb freqüents però moderades pertorbacions ha estat, de fet, beneficiós per a molts organismes (Farina 1997, Blondel & Aronson 1999).

Tot i això, durant el segle XX, els països Euro-Mediterranis han patit una uniformització del antic mosaic paisatgístic. D'una banda, l'abandonament dels usos tradicionals de la terra a les regions muntanyoses degut als seus beneficis marginals ha implicat l'extensió dels boscos i comunitats arbustives (Preiss et al. 1997). L'acumulació de combustible ha contribuït a augmentar el risc d'incendis i, conseqüentment, ha tingut un paper rellevant en l'increment de la superfície cremada (Le Houerou 1990). A més, el progressiu deteriorament climàtic durant la segona meitat del segle, caracteritzat per un augment de la temperatura i una disminució de la humitat, també ha contribuït a l'expansió de les superfícies afectades pel foc (Piñol et al. 1998). D'altra banda, l'activitat humana s'ha intensificat a les valls fèrtils i a les costes, on els fragments de vegetació natural han esdevingut cada cop més escassos i isolats. Les dades disponibles suggereixen que tots dos extrems, tant l'abandonament com la intensificació de l'ús de la terra, estan comportant una reducció de la diversitat biològica (Blondel & Aronson 1999).

La recerca ecològica en aquest escenari tant complex va començar no fa gaire temps i encara se sap poca cosa sobre la resposta dels organismes als règims de pertorbació tradicionals o recents, que condueixen a patrons de paisatge tant diferents. Això representa, per tant, un repte pels investigadors, que no només han d'intentar entendre el paper de les pertorbacions en la vida salvatge sinó també subministrar pautes factibles que serveixin per a fer compatibles el maneig del territori i la conservació biològica.

Els ocells han estat àmpliament utilitzats per al seguiment de les alteracions dels hàbitats i els paisatges ja que són relativament fàcils de censar i són bons i coneguts indicadors biològics (Furness & Greenwood 1993). A més, moltes espècies d'ocells mediterrànies estan en un estat de conservació vulnerable o en perill (Tucker & Heath 1994) i, per tant, els factors ambientals que afecten a aquestes espècies estan rebent una atenció especial per part dels investigadors i dels gestors del medi natural. Dins aquest marc, aquesta tesi intenta contribuir al coneixement de les relacions entre els ocells i les pertorbacions en els ambients mediterranis i, concretament, es centra en els efectes del foc i de la fragmentació en els ocells.

El foc i els ocells mediterranis

Tot i l'alta freqüència de focs en paisatges mediterranis, l'estudi dels seus efectes en els ocells ha estat pobrament desenvolupat si el comparem amb altres regions del món (Prodon & Pons 1993). No obstant, durant les darreres dues dècades s'han aportat dades valuoses, especialment a partir dels estudis portats a terme al sud de França per R. Prodon i altres.

Degut a la seva capacitat de volar, les ocells poden sovint evitar l'impacte directe de les flames a través del seu desplaçament cap als hàbitats adjacents no afectats pel pas del foc. Tot i això, la dràstica modificació de l'hàbitat té importants conseqüències en la recolonització de l'àrea cremada. Algunes espècies són capaces de retornar als territoris cremats durant la primera estació reproductora després del incendi, gràcies a la seva forta filopàtria, l'alta tolerància als canvis en l'hàbitat i a la presència d'arbres morts dempeus, però abandonen progressivament els territoris de nidificació i no tornen a aparèixer fins que la vegetació torna a assolir l'aspecte forestal (Prodon et al. 1987, Pons & Prodon 1996). Sense comptar amb aquestes casos excepcionals, la successió post-incendi de les comunitats d'ocells està estretament lligada amb la recuperació de la vegetació, començant primer amb les espècies d'espais oberts, seguit de les espècies d'hàbitats arbustius i, finalment, de les forestals (Prodon et al. 1984). Dins d'aquest marc, i des d'una perspectiva conservacionista, cal remarcar el fet que als ambients mediterranis, els estadis successionals inicials proveeixen hàbitats adequats per a moltes espècies d'ocells vulnerables (Rocamora 1997), mentre que les comunitats d'ocells de zones boscoses estan essencialment formades per espècies comunes i àmpliament distribuïdes per tot el Paleartic occidental (Blondel & Farré 1988).

La intervenció humana en el procés successional ha estat estudiada també en relació amb l'extracció de fusta, la qual provoca apreciables desviacions en el recanvi espontani de les comunitats d'ocells desprès del foc (Llimona et al. 1993, Izhaki &

Adar 1997). Finalment, i en relació al interès en augment que les cremes prescrites tenen com a tècnica per a prevenir els grans focs (Miller & Hardy 2000), Pons (1998) va estudiar els efectes d'aquestes petites cremes i va mostrar que l'increment de la heterogeneïtat de l'hàbitat no només permetia la persistència de totes les espècies que habitaven la zona abans del foc, sinó que fins i tot afavoria l'establiment de passeriformes d'espais oberts.

Fins ara, la majoria dels treballs sobre els efectes del foc en els ocells a la conca Mediterrània s'han dut a terme a la zona mèsica "meso-mediterrània" (veure marc 2) (Prodon et al. 1984, Prodon et al. 1987, Vicente 1991, Pons & Prodon 1996, García 1997) i són escasses les dades provinents de la zona més seca i càlida "thermo-mediterrània", la qual està encara més afectada pels focs. Dins d'aquest context geogràfic, aquesta tesi analitza alguns patrons espacials i temporals de les comunitats i d'ocells relacionades amb els incendis.

Fragmentació i ocells en paisatges mediterranis

L'estudi dels efectes de la fragmentació en els ocells en paisatges mediterranis ha estat també pobrament desenvolupat fins fa poc. Durant el darrers 10 anys un grup d'investigadors de la Universidad Complutense de Madrid encapçalats per J.L. Tellería i T. Santos ha obtingut una considerable quantitat de dades estudiant fragments forestals de la Meseta Ibèrica.

Tal i com s'ha vist en altres regions temperades del món (e.g. Hinsley et al. 1995, Bellamy et al. 1996), Díaz et al. (1998) van trobar que la mida del fragment era el factor més important que hi havia al darrera dels patrons d'ocupació dels fragments forestals ibèrics. Estudiant els efectes de la fragmentació en àrees amb una cobertura forestal total baixa, aquests autors també van mostrar que els ocells forestals estaven negativament influenciats pel grau d'isolament dels fragments. Aquest resultat és consistent amb els d'Andrén (1994), qui va suggerir que aquest efecte apareixia en paisatges que contenien menys d'un 30% de l'hàbitat en qüestió. Però, tal i com ja suggerien Mönkönen i Reunanen (1999), aquest patró no pot ser generalitzat perquè en una altre estudi portat a terme en un paisatge amb una cobertura forestal inferior al 20%, Tellería i Santos (1999) no van trobar cap efecte significatiu de l'isolament. Un altre resultat interessant és el del paper de les densitats ecològiques en la capacitat dels ocells per ocupar els fragments, essent les espècies més abundants les que tendeixen a ocupar un rang més ampli de mides de bosc, i les més escasses les que tendeixen a residir només en els fragments més grans (Díaz et al. 1998, Tellería & Santos 1999). Per últim cal dir que Tellería & Santos (1997) van trobar que la persistència interanual en la ocupació d'un fragment estava directament relacionada amb l'abundància de l'espècie.

Així doncs, les dades disponibles suggereixen que, a pesar de la particular història de fragmentació forestal en la conca mediterrània, les espècies forestals responen a aquesta pertorbació de manera similar a com ho fan en altres regions. Amb tot, fins ara la major part dels estudis s'han centrat en arxipèlags forestals localitzats enmig dels camps de cereals de la Meseta Ibèrica i no hi ha dades disponibles en matrius arbustives, les quals són molt comunes a moltes regions costaneres de la conca mediterrània. Tenint en compte la importància del tipus de matriu per als ocells que viuen als fragments isolats (Pearson 1993, McGarigal & McComb 1995, Sisk et al. 1997, Saab 1999), vaig considerar interessant estudiar la fragmentació forestal dins matrius arbustives (tant naturals com agrícoles) del nord-est peninsular. Aquesta tesi, a més, es centra en els poc estudiats efectes de fragmentació en boscos de pi blanc, els quals constitueixen un dels tipus de bosc més freqüents als paisatges que envolten el mar Mediterrani.

Marc 1: Espècies d'ocells

Aquesta tesi tracta del conjunt de la comunitat d'ocells, amb la única excepció dels rapinyaires i de les espècies que mengen al vol, com les orenetes i els falciots. La riquesa, l'abundància i ordenacions ecològiques de les espècies han estat àmpliament utilitzades com a descriptors de la comunitat d'ocells per a testar diferents prediccions. Tot i això, les respostes de poblacions específiques també han estat considerades quan ha estat apropiat per a testar les hipòtesis corresponents (Capítol 3 i Capítol 6). La major part del treball de camp ha estat portat a terme durant la temporada de nidificació però una part ha estat fet durant la d'hivernada. No s'ha intentat monitoritzar les relacions existents entre les pertorbacions en l'hàbitat i els migrants de llarga distància perquè aquests ocells resideixen als hàbitats mediterranis només durant breus períodes a la tardor i a la primavera. Encara que aquest darrer grup també pot estar influenciat per les pertorbacions estudiades, el curt període que aquestes espècies passen a la zona i la seva alta mobilitat dificulten extraordinàriament l'estudi de la resposta d'aquestes espècies a les pertorbacions.

Marc 2: Àrea d'estudi

La major part de la recerca que havia estat realitzada sobre els efectes de les pertorbacions en ocells mediterranis havia estat duta a terme a la zona meso-Mediterrània, que es caracteritza per la presència de boscos d'alzina (Blondel & Aronson 1999). Això contrasta amb l'escassetat de dades provinents de la més càlida i seca zona thermo-Mediterrània, que està caracteritzada per la presència de màquies (actualment molt degradades) d'ullastre (*Olea europaea*), garrofer (*Ceratonia siliqua*), llentiscle (*Pistacia lentiscus*) o margalló (*Chamaerops humilis*) (Blondel & Aronson 1999). Aquesta tesi està bàsicament centrada en la segona zona, però en els estudis de fragmentació es situa a cavall entre les dues zones. El treball de camp es va realitzar a les muntanyes i valls de litologia calcària del nord-est peninsular, entre les ciutats de Tortosa i Barcelona. Específicament, la major part del treball de camp (cinc capítols) es va fer exclusivament al Parc Natural del Garraf.

Objectius d'aquesta tesi

El principal objectiu d'aquesta tesi és analitzar com el foc i la fragmentació afecten als ocells en paisatges mediterranis. Cada capítol d'aquest treball planteja qüestions i hipòtesis sobre les respostes ecològiques dels ocells a aquestes pertorbacions. La relació existent entre els ocells i els canvis en els hàbitats és actualment un dels principals objectius quant la conservació dels ocells (Tucker & Evans 1997) i, per tant, sempre que els resultats són considerats rellevants per a la conservació, s'ha pres una atenció especial per mostrar les contribucions d'aquesta recerca a la gestió de la natura. A continuació s'especifiquen els objectius d'aquesta tesi.

El primer objectiu d'aquesta tesi va ser analitzar la successió de la comunitat d'ocells després del foc en una zona thermo-mediterrània. Vaig portar a terme aquesta recerca al Parc Natural del Garraf i, donat que l'eixutesa de la zona pot fer lenta la recuperació de la vegetació, vaig hipotetitzar que la successió ornítica estaria també caracteritzada per una lenta recuperació de la riquesa i l'abundància, i, a la vegada, per un lent canvi des de comunitats dominades per espècies de llocs obert a comunitats dominades per espècies arbustives (Capítol 2). A més, em vaig centrar en dues espècies (la tallareta cuallarga *Sylvia undata* i el tallarol capnegre *Sylvia melanocephala*) per analitzar si la dinàmica post-incendi podia estar influenciada per les tendències poblacionals a una escala més gran que l'hàbitat pertorbat (Capítol 3).

Els grans incendis causen una pèrdua d'heterogeneïtat paisatgística ja que converteixen el mosaic vegetal en una homogènia àrea cremada. En el capítol 4, vaig estudiar la variabilitat espacial de les comunitats d'ocells en zones afectades pels focs en un grau variable. Específicament, em vaig fer dues preguntes principals: són les comunitats d'ocells més espacialment uniformes als llocs cremats que als no cremats? Responen de manera semblant les espècies de llocs cremats i de llocs no cremats als canvis en l'estructura de l'hàbitat?

Està generalment acceptat que els sistemes madurs contenen una comunitat d'ocells més estable que els pertorbats. Per tant, vaig hipotetitzar que la comunitat d'ocells dels llocs cremats patien majors canvis estacionals que les que vivien en àrees no cremades. Es van fer censos d'ocells nidificants i hivernants al Parc Natural del Garraf per a testar aquesta hipòtesi (Capítol 5).

L'estudi dels efectes dels canvis en l'hàbitat en els ocells ha estat normalment basat en la concepció que l'abundància d'ocells és un indicador adequat de les respostes de la població a les transformacions de l'hàbitat. No obstant, les estimes d'abundància no donen una informació directa sobre la qualitat dels individus en les seus hàbitats (Van Horne 1983, Wiens 1989). Per aquesta raó, vaig realitzar un estudi per determinar si els individus d'una espècie capaç d'habitar tant zones cremades com no cremades (el tallarol capnegre *Sylvia melanocephala*), mostrava diferències en la seva condició física en aquestes dues zones. Aquesta investigació es va portar a terme utilitzant mesures d'asimetria obtingudes de les rectrius d'aquests ocells(Capítol 6).

Tal i com s'ha explicat, els focs tenen un paper important com a fragmentadors de la massa forestal. El capítol 7 d'aquesta tesi planteja, per primera vegada, la qüestió de les conseqüències dels incendis en els ocells que viuen en els fragments de bosc que queden sense cremar després del pas del foc. Tenint en compte el paper que aquesta pertorbació ha tingut en les paisatges mediterranis, Vaig hipotetitzar un moderat impacte d'aquest tipus de fragmentació en aquestes espècies.

Finalment, el darrer capítol d'aquesta tesi està dedicat a analitzar els factors que determinen la comunitat d'ocells en boscos de pi blanc envoltats per vinyes, amb un especial èmfasi en les influències de la mida del bosc, el grau d'isolament, el paper dels corredors riberencs i la composició i estructura de la vegetació (Capítol 8).

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Bird community succession after fire in a dry Mediterranean shrubland[1]

Abstract

Animal succession dynamics and restoration of community structure after fire are related to vegetation recovery, which is highly influenced by climate. As the thermo-Mediterranean life zone is characterised by stronger dryness conditions than other Mediterranean zones, we hypothesised that the bird community succession here is very slow. We used the point-count method to census birds from the first to the sixth breeding seasons after fire in burnt and unburnt shrublands of the Northeast Iberian Peninsula. Bird richness and abundance increased rapidly and even exceeded the values of the unburnt zone the sixth year after fire. Nevertheless, in the burnt zone, the expected change from communities dominated by open-space species to communities dominated by shrubland species was not detected and high proportions of the former were maintained in the species pool throughout all the study period.

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[1] With Lluís Brotons, Rodrigo del Amo & Santiago Llacuna. University of Barcelona. Submitted.

INTRODUCTION

The understanding of ecosystem response to perturbations has greatly interested biologists and wildlife managers (Meffe *et al.* 1997). In particular, the effects of fire in bird communities has focused researchers' attention all over the world, but, despite the high frequency of this disturbance in Mediterranean ecosystems, the post-fire bird studies are not particularly abundant in these systems (Prodon & Pons 1993). The studies of post-fire bird successions in Mediterranean habitats were initiated in California by Lawrence (1966), who showed that flames did not kill birds, but rather forced relocation in appropriate adjacent habitats and that grassland bird species colonised the burnt areas. Prodon *et al.* (1984) started these types of successional studies in the Mediterranean Basin and showed that the recovery of bird populations was dependent on how vegetation regenerated. Thus, bird communities reached pre-fire species composition faster in areas where trees sprouted from main branches than in those where fire killed the aerial parts of plants. In spite of such parallelism, Prodon *et al.* (1987) found that, as a consequence of the bird philopatry and the habitat tolerance of some forest species, bird recovery could be temporally non-equilibrated with vegetation regeneration in some burnt habitats. Later, Pons & Prodon (1996) reported an early and continuous use of burnt shrublands and explained the moderate effects of fire on bird communities as a consequence of mechanisms such as site tenacity and the persistence of patches of unburnt vegetation.

Nevertheless, all these studies have been carried out in the "meso-Mediterranean" life zone, which has a moderate climate and is characterised by evergreen oaks such as Holm-oak (*Quercus ilex*) and Cork-oak (*Quercus suber*) as dominant tree species (Blondel & Aronson 1999). No attempt has been made to study bird successions after fire in the dryer "thermo-Mediterranean" life zone, which is characterised by dense coastal woodlands of Wild Olive Trees (*Olea europaea*), Lentisk (*Pistacia lentiscus*), Mediterranean Dwarf Palm (*Chamaerops humilis*) and a variable abundance of Aleppo Pines (*Pinus halepensis*) (Blondel & Aronson 1999). Furthermore, these plant communities are believed to recover slowly after fire since water limitation is one of the key factors in the successional dynamics of Mediterranean vegetation (Zavala *et al.* 2000). In addition, Stanton (1986) indicated that bird community dynamics after fire in dry Mediterranean coastal shrublands of California differed notably from that of the more humid chaparrals.

The aim of this work was to study the succession of bird communities in a thermo-Mediterranean shrubland. We hypothesised that, given the dryness of this area, avian succession after fire would be characterised by a slow recovery of richness and abundance and by a slow change from communities dominated by open-space bird species to communities dominated by shrubland bird species.

METHODS

Study area

This study was carried out in the Garraf Natural Park, situated 20 km to the south of the city of Barcelona (NE Iberian Peninsula). The study area (41º 15' N, 1º 55' E) consists of low hills and small valleys located between 100 and 500 m.a.s.l. Yearly average precipitation ranges from 450 to 650 mm, but the karstic lithology of these hills provides only skeletic soils which implies very dry conditions for plant communities. In fact, the Garraf Massif represents the northern border of the thermo-Mediterranean life zone in the Iberian Peninsula.

After a long period only slightly interrupted by small fires, two extensive wildfires have profoundly marked the latest decades: the first burnt 10000 ha in 1982 and the second, which burnt entirely over the first, affected 5000 ha in 1994. This last fire was very intense and thus, the total area covered by the small remnant patches of unburnt vegetation accounted for less than 2% of the 5000 ha. Hereafter and to simplify the terminology with respect to the second fire, the two zones are called burnt zone (the zone burnt in 1994) and unburnt zone (the zone not burnt in 1994). The simultaneous monitoring of burnt and unburnt control zones represents one of the most suitable ways to study successions after fire since it incorporates a parallel control in order to eliminate the influence of temporal variations unrelated to the occurrence of fire (Prodon & Pons 1993). Similarities between the two zones were not tested before the fire event. Nevertheless, we did not find significant differences in relief, landscape characteristics and floristic composition between both zones. Moreover, the zone burnt in 1994 was mostly surrounded by the unburnt one. Therefore, we considered the unburnt zone as a suitable control to study the temporal dynamics of bird communities occurred in the burnt one. The unburnt control zone was dominated by shrub species, which, sorted with respect to decreasing abundance, were *Quercus coccifera, Pistacia lentiscus, Phillyrea latifolia, Rosmarinus officinalis, Olea europaea* and *Chamaerops humilis*. These shrubs formed a 1-m tall layer that covered from 70% to 90% of the surface. Scattered young pines (*Pinus halepensis*) (8% cover) reached a mean of 3 m tall and grasses (mainly *Brachypodium restusum*) cover about 20%. Finally, protruding karstic rocks covered almost 9% of surface on average.

Bird counting

The censuses were carried out in the burnt and in the unburnt zones during the breeding seasons of 1995, 1997, 1998 and 2000. Point-counts to infinity with no estimation of distance were employed to assess the abundance of bird species (Bibby *et al.* 1992). We selected 35 counting stations (19 in the burnt zone and 16 in the unburnt), locating them at a minimum 400-m distance from each other to avoid pseudoreplication. We also assured that the area around each station was homogeneous and did not include farmland, urbanised areas or cliffs. Thus a total of 140 censuses was carried out during the study period.

Counting was conducted in the morning, during the period of maximum activity for birds, starting 1 h after dawn and 5 min after the arrival at the station. Point counts taken by other authors have ranged from 5 to 20 min, but following the recommendations of Fuller & Langslow (1984), 10 min was chosen as a compromise. Raptors, aerial feeders (such as swallows, swifts or bee-eaters) and crepuscular species were not taken into account in the calculations because this method is not appropriate for assessing their abundance (Bibby *et al.* 1992). We only considered in this paper species that bred in the study stations. Therefore, very mobile species that used the habitat as a feeding site but were not reported to breed in the stations at any time (such as finches, doves and woodpeckers) were excluded from the analyses. We carried out bird censuses exclusively under uniformly good weather conditions, without rainfall or wind.

Data analysis

Bird abundance and richness were assessed respectively as the total number of individuals and species detected at each station during 10 minutes. Classical measurements of diversity such as the Shannon index H’ were not assessed because they are positively correlated with richness and the supplementary information conveyed by H’ is usually low in breeding bird communities (Prodon 1992). Correspondence analysis (CA) was used to obtain a main factor that summarised the principal ordination of bird species and was interpreted *a posteriori* regarding the knowledge about the ecology of the species concerned. CA is a descriptive/exploratory technique designed to analyse multi-way tables containing some measure of correspondence between the rows and columns (Greenacre 1984). This analysis attributes scores to both species and stations so that the correlation between station scores and species scores is maximal, given the best "correspondence" between species and stations (Prodon 1992). We used repeated measures ANOVA and the post-hoc Tukey Honest Significant Difference (HSD) Test (Sokal & Rohlf 1995) to analyse variations on bird community descriptors (richness, abundance and the main factor from the CA) in relation to zone (burnt and unburnt) and time since fire. All statistical analyses were run with Statistica Statsoft, Inc 1999.

RESULTS

Considering the whole of the study period, bird richness did not differ between the burnt and the unburnt zones ($F_{1,33}$=0.39, P=0.536). However, bird richness was not constant across years ($F_{3,99}$=4.17, P<0.01). This temporal variation in bird richness was not homogenous and was greatly determined by the zone under study ($F_{3,99}$=10.74, P<0.001). Richness was higher in the unburnt zone than in the burnt one during the first year after fire, did not differ between zones from the second to the fourth year after fire and became higher in the burnt zone in the sixth year after fire (Fig. 1).

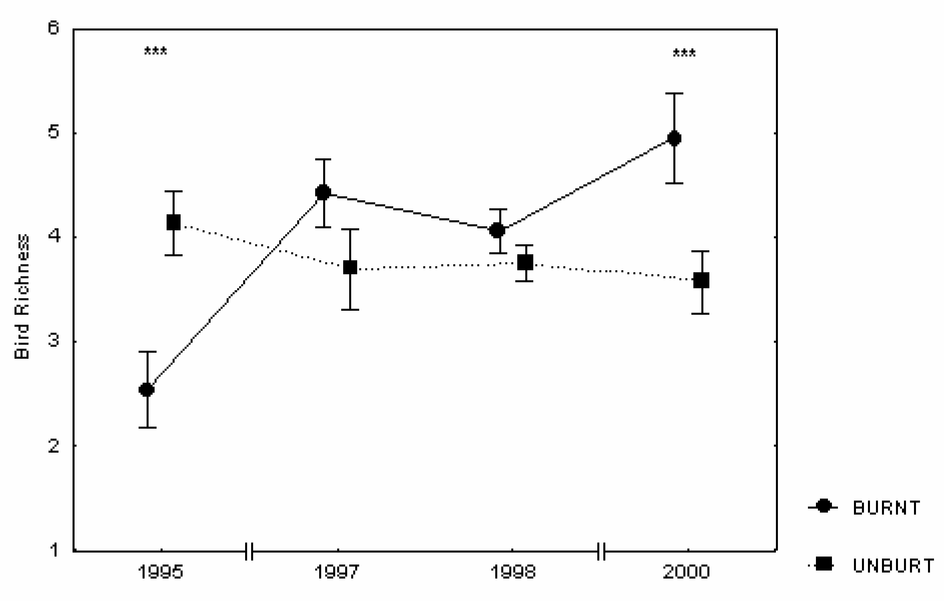

Figure 1. Variation in bird richness after 1994 fire. Bars indicate Standard Error. According to Tukey HSD test, significant differences between zones in a year are marked *** in the top of the figure.

Similarly, bird abundance did not differ between zones ($F_{1,33}$=1.01, P=0.321), but it differed between years ($F_{3,99}$=4.63, P<0.01) and the interaction between the zone and the year was also highly significant ($F_{3,99}$=9.74, P<0.001). As for bird richness, the abundance was higher in the unburnt zone than in the burnt zone during the first year after fire but this difference disappeared from then until the sixth year after fire, when bird abundance became higher in the burnt zone (Fig. 2).

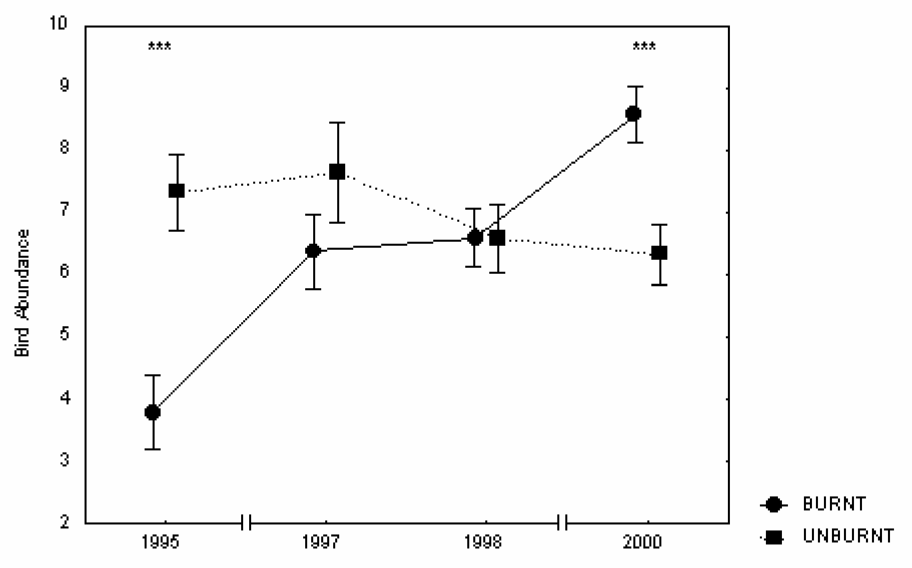

Figure 2. Variation in bird abundance after 1994 fire. Bars indicate Standard Error. According to Tukey HSD test, significant differences between zones in a year are marked *** in the top of the figure.

A total of 18 breeding species were found in the set of stations during the study period (Table 1). The first factor (F1) obtained with the correspondence analysis, which represented 13.4 % of total data variance, corresponded to an ecological gradient from open-space bird species (positive values) to shrubland bird species (negative values). The extreme negative values represented forest species that managed to breed in stations with a high shrub development (Table 1). Therefore, variations of F1 corresponded to the variations from communities dominated by a set of open-space species to communities dominated by a set of shrubland species. Independently on the studied year, the community composition was clearly characterised by open-space birds in the burnt stations and by shrubland species in the unburnt ones ($F_{1,32}$=20.06, P=0.001) (Fig.3). However, F1 remained very stable during the studied period (five years) in both, burnt and unburnt zones, and no significant trend was found neither between years ($F_{3,96}$=0.30, P=0.827) nor in the interaction between years and zone ($F_{3,96}$=0.56, P=0.645) (Fig. 3). Therefore, we did not detect a change from communities dominated by open-space species to communities dominated by shrubland species from the first to the sixth breeding season after 94'fire.

Table 1. Relative abundance of the bird species found in the two studied zones (the burnt zone / the unburnt zone), expressed as the mean number of individuals detected in a station during the 10 min. census. The score of the first factor of the correspondence analysis (F1) for each bird species is also shown.

Bird species		**1995**	**1997**	**1998**	**2000**	**F1**
Tawny Pipit	*Anthus campestris*	0.05 / 0	0.21 / 0.06	0.16 / 0.13	0.21 / 0	1.51
Ortolan Bunting	*Emberiza hortulana*	0.11 / 0.13	0.11 / 0	0.05 / 0.13	0.26 / 0	0.93
Thekla Lark	*Galerida theklae*	0 / 0	0.11 / 0	0.11 / 0	0.16 / 0	0.88
Corn Bunting	*Miliaria calandra*	0.21 / 0.13	0.37 / 0	0 / 0	0.26 / 0	0.78
Rock Thrush	*Monticola saxatilis*	0.05 / 0.30	0.11 / 0.06	0 / 0.13	0.05 / 0.06	0.64
Southern Grey Shrike	*Lanius meridionalis*	0.21 / 0.13	0.42 / 0.19	0.37 / 0.13	0.32 / 0.25	0.62
Black-eared Wheatear	*Oenanthe hispanica*	0.74 / 0.19	1.05 / 0.31	1.05 / 0.13	0.79 / 0.12	0.56
Woodchat Shrike	*Lanius senator*	0.26 / 0.06	0.26 / 0	0.05 / 0	0.11 / 0	0.50
Red-legged Partridge	*Alectoris rufa*	0.47 / 0.13	0.95 / 0.31	0.53 / 0.06	0.16 / 0.13	0.40
Stonechat	*Saxicola torquata*	0.42 / 1.06	0.53 / 0.75	1.00 / 0.50	1.21 / 0.50	0.35
Dartford Warbler	*Sylvia undata*	0.68 / 1.94	1.32 / 2.19	2.37 / 2.00	3.11 / 1.82	-0.14
Sardinian Warbler	*Sylvia melanocephala*	0.26 / 1.44	0.79 / 2.00	0.63 / 1.81	1.58 / 2.62	-0.37
Great Tit	*Parus major*	0.05 / 0.44	0.11 / 0.25	0 / 0.06	0.11 / 0.25	-0.77
Rock Bunting	*Emberiza cia*	0 / 0	0 / 0.13	0 / 0.13	0 / 0	-0.80
Blackbird	*Turdus merula*	0.16 / 0.75	0.05 / 0.56	0.26 / 1.00	0.26 / 0.19	-1.01
Wren	*Troglodytes troglodytes*	0 / 0.38	0 / 0.19	0 / 0.25	0 / 0.25	-1.40
Long-tailed Tit	*Aegithalos caudatus*	0 / 0	0 / 0.44	0 / 0	0 / 0	-1.79
Nightingale	*Luscinia megarrhynchos*	0 / 0.19	0 / 0.19	0 / 0.13	0 / 0.13	-2.21

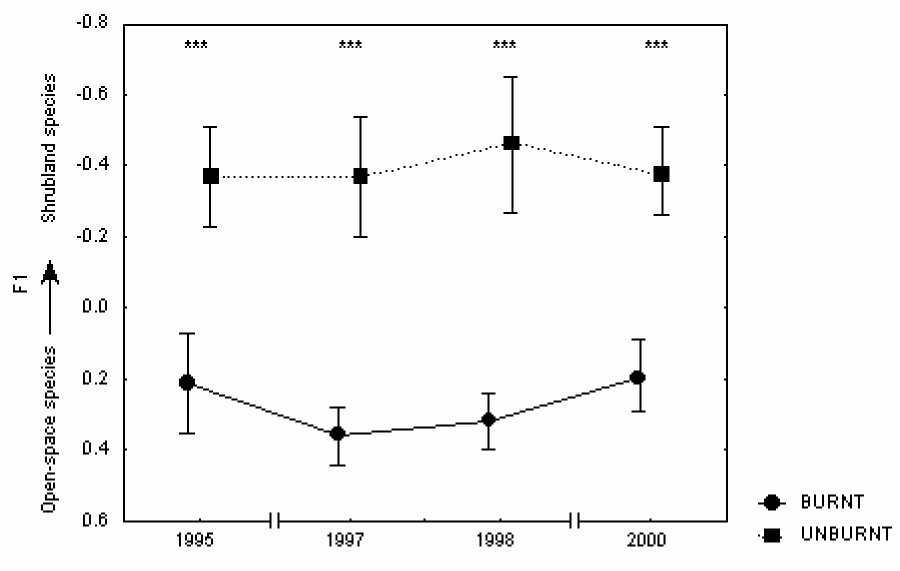

Figure 3. Variation in the gradient open-space species / shrubland species (F1) after 1994 fire. Bars indicate Standard Error. According to Tukey HSD test, significant differences between zones in a year are marked *** in the top of the figure.

DISCUSSION

Our results showed that bird richness and abundance increased rapidly after 94'fire and even exceeded the values reported in the unburnt zone the sixth year after fire, whereas these parameters did not change in the unburnt zone. These results reject our initial hypothesis of a slow recovery of these parameters in this dry "thermo-Mediterranean" area and reported comparable speed as found in the bird successions studied in more humid “meso-Mediterranean” burnt shrublands (Prodon *et al.* 1984). Trabaud & Papió (1987), studying the post-fire vegetation recovery in the Garraf Natural Park after 82’ fire found a really slow recuperation of pre-fire vegetation. However, they reported a rapid plant growth during the first two years after fire followed by an extraordinary slowing down of the process from then on. Therefore, the rapid vegetation recovery soon after fire seemed to be enough for birds to reach, and even exceed, pre-fire abundance and richness.

Low richness and abundance in burnt areas one year after fire, compared with unburnt controls, are common in post-fire studies in the Mediterranean Basin (e.g. Prodon *et al.* 1987, Pons & Prodon 1996, García 1997). More unusual is that richness and abundance surpass the values observed in the unburnt control as succession continued. Nevertheless, Prodon *et al.* (1984) also reported higher bird richness in French burnt shrublands than in unburnt controls. As suggested by these authors, this event seems to indicate that the number of ecological niches per counting station was higher in these burnt shrublands than in neighbour unburnt ones, which may be related to a higher heterogeneity of habitat structure in burnt stations. This association between spatial heterogeneity and bird richness has been repeatedly reported (Wiens 1989). In our case, six years after fire, isolated shrubs have grown enough to form a patchily mosaic with grasses and stony grounds, which contrasts with the higher uniformity of habitat within unburnt stations. However, the spatial heterogeneity of landscapes are usually scale-dependent (Forman & Gordon 1986). In fact, we analysed the spatial variations of habitat structure and avifauna in our two study zones and found that the unburnt stations differed among them more than the burnt ones (unpubl. data). This suggests that, in a large scale (zone), the area affected by fire is more homogeneous than the unburnt, whereas in small scale (stations) the relationship is opposite.

Although, theoretically, all secondary succession such as that provoked by fire implies a progressive change from communities dominated by open-space birds to communities dominated by shrubland and later forest birds (Helle & Mönkkönen 1990), our results do not fit well with this statement and we found a surprising absence of this type of temporal shift from the first to the sixth year after fire. Prodon *et al.* (1987) also reported an absence of change in the open-space species / shrubland species gradient in burnt Holm-oak forests from the first to the fifth years after fire. These authors explained this stability by two antagonistic effects: on one hand, the departure of open vegetation bird species (larks, buntings, wheatears...) as succession proceeded and, on the other, the simultaneous departure of certain tenaceous forest species which managed to inhabit recently burnt areas (Great Tit, Chaffinch...). Nevertheless, this explanation does not seem valid for our case. Open vegetation species remained in the burnt zone during all the study period, and the few forest species present during the first breeding season after fire (Great Tit and Blackbird) did not disappear afterwards. However, as in Prodon *et al.*’s work, the temporal stability of this gradient can be explained by a compensation between open and shrubland species. In our case, instead of a simultaneous departure of species belonging to opposite ecological gradients as succession proceeded, we found a simultaneous increase in the occurrence of shrubland species (such as Dartford Warbler and Sardinian Warbler) and open-space species (such as Thekla Lark and Tawny Pipit). This pattern is consistent with the progressive increase in bird richness and abundance observed in the burnt zone. The progressive increase in shrubland species can be easily explained by the growth of shrubs. Open-space species also had their lowest numbers during the first successional stages and increased when habitat began closing. We hypothesised that this apparent contradiction can be explained in relation with the colonisation process of the recently burnt zone from neighbour sink areas. At a landscape level, the burnt zone was mostly surrounded by closed shrublands that were not suitable for open-space species, which, after fire, had to spread to the 5000-ha burnt zone. Thus, open-space species did not become abundant during the first years after fire, although they probably increased afterwards helped by local reproduction in the burnt zone.

Our findings also have interesting implications in bird diversity conservation in Mediterranean areas. In fact, 75% of bird species inhabiting the burnt zone are considered to be either decreasing or in a vulnerable situation in Europe (Tucker & Heath 1994). These bird species are all open-space species for which habitat loss might be the most relevant threat in the Mediterranean Basin (Rocamora 1997). Therefore, the permanence of proper populations of these species at least during the first six years after fire suggests that these burnt dry Mediterranean shrublands may represent appropriate habitats for their conservation. Several of these species were also present in the unburnt control (which in fact was also burnt in 1982), but their abundance was lower here than in the burnt zone, which suggests that the latter is a more suitable habitat. From a management perspective, large fire prevention practices carried out to reduce the amount of combustible using prescribed burning may contribute to maintain high quality habitats for these species. In the Mediterranean Southern France, Pons (1998) reported a colonisation of open-space species (e.g. Tawny Pipit and Woodlark) after a prescribed fire, but it was followed by a fast decrease of their densities as early as the second year after fire, when the shrub cover was regenerated enough. Our results suggest that these types of management policies could be of great interest in dry Mediterranean shrublands, where these species do not seem to decrease rapidly after fire.

In conclusion, our results suggest that the bird community succession after fire in the thermo-Mediterranean life-zone is, at least during the first years after fire, characterised by a fast increase in bird richness and abundance, but not by a clear change from communities dominated by open-space species to communities dominated by shrubland species. However, further studies are needed to complete the hypothetical progression towards a shrubland and forest species composition during following years. The interest in these long-term studies is stressed by current fire frequency and by the regional aspects of climate change. Recurrent fires may reduce the sprouting capacity of many Mediterranean plants, impede the storage of enough seeds during the pre-fire stage and degrade soils via erosion (Le Houérou 1981, Blondel & Aronson 1999). As a result, plant succession may be blocked and thus, open vegetation formations become permanent, even if fire frequency decreases. During the last decades, this phenomenon has taken a predominant role in many areas of the Iberian Mediterranean coast (Carreira & Niell 1992, Puigdefàbregas & Mendizabal 1998), and thus, the bird communities of these areas may remain dominated by open-space species. Moreover, several models of climate change are also suggesting an increase in the aridity of this area (Moreno & Oechel 1995), thus affecting the recovery of burnt vegetation and hence, indirectly, birds. However, this hypothetically dramatic framework may favour bird species that are considered as threatened, which gives an idea of the complexity of the problem from a conservation point of view.

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Factors influencing post-fire dynamics of Sardinian and Dartford Warblers in Mediterranean shrublands

Abstract

We studied the post-fire dynamics of two Mediterranean warblers (the Sardinian (*Sylvia melanocephala*) and the Dartford Warbler (*Sylvia undata*)) to determine whether these were influenced by local habitat recovery or by external population trends unrelated to the occurrence of fire. We used the point-count method to survey warblers from the first to the sixth breeding seasons after fire in burnt and unburnt control zones of the Iberian Peninsula. Both species increased similarly in the burnt zone until the fourth year after fire, but the Dartford Warbler increased faster than the Sardinian Warbler from then on. Six years after fire, the abundance of the Dartford Warbler was even higher in the burnt zone than in the control, where the population of this species remained constant during the study period. In contrast, a parallel increase in the populations of Sardinian Warbler in both zones was observed, thus suggesting that processes other than fire were profoundly involved in the dynamics of this species in the burnt zone. Our results indicate that the post-fire dynamics of these two species greatly differ, the Dartford Warbler being highly influenced by local habitat changes in the burnt zone and the Sardinian Warbler by population trend on a larger scale than the disturbed habitat.

[1] With Rodrigo del Amo, Lluís Brotons & Santiago Llacuna. University of Barcelona.
Ornis Fennica 2001 (in press).

INTRODUCTION

Fires are a frequent disturbance in the Mediterranean area and are known to play a key role in the spatial and temporal dynamics of forest and shrubby systems (Blondel & Aronson 1999). The study of bird succession after fire in the Mediterranean Basin has focused on species turnover and its close association with vegetation recovery (e.g. Prodon *et al*. 1984, Prodon *et al*. 1987, Pons & Prodon 1996, Izhaki & Adar 1997). Prodon and Pons (1993) pointed out the importance of simultaneously monitoring burnt and unburnt control zones to eliminate the influence of temporal variations unrelated to the occurrence of fire. Therefore, as well as changes in the local habitat, factors with an effect on a larger scale, such as fluctuations in the nearby “source" population, mortality associated with migration, changes in predation or parasitism rates, climatic oscillations and so on, may influence local bird numbers (Wiens 1989). Several studies have reported how regional population trends greatly affect local bird abundance independently of habitat modifications (e.g. Hickey & Brittingham 1991, Böhning-Gaese & Bauer 1996, Bellamy *et al*. 2000). However, to our knowledge, to date no study has focused on the influences of regional population trends in the post-fire succession of burnt areas.

Two Mediterranean warblers, the Sardinian Warbler (*Sylvia melanocephala*) and the Dartford Warbler (*Sylvia undata*), often coexist in Western Mediterranean shrublands, although the former prefer low matorrals, whereas the latter seems to be favoured by medium and tall ones (Cody & Walter 1976, Martin & Thibault 1996). The post-fire abundance patterns of these shrub-dwelling species is usually characterised by their absence during the first breeding season after fire and by a gradual increase in their numbers afterwards (Prodon & Lebreton 1983, Prodon *et al.* 1987, López & Guitian 1988, Llimona *et al.* 1993). Nevertheless, the temporal variations of these two warblers in burnt zones may be affected by temporal dynamics on a larger scale. Available data suggest that the population trends of these two warblers differ at a regional level. In contrast to the stability of the populations of Sardinian Warbler, the populations of Dartford Warbler have undergone a slow but progressive decrease since the 1970s in Spain (which has 75-95% of the world population of this species) (Tucker & Heath 1994). Furthermore, the current tendencies of land abandonment and progressive afforestation in European countries in the Mediterranean have been reported to affect the Dartford Warbler negatively and the Sardinian Warbler positively (Preiss *et al.* 1997). Therefore, these two species of the genus *Sylvia* are an ideal set with which to study whether post-fire dynamics are influenced by factors other than local changes in habitat after fire.

Within this context, we propose two possible scenarios. First, if vegetation recovery determines the post-fire dynamics of the species, we hypothesise (1) a positive and strong effect of time since fire on the population trend in burnt areas, independently of that in unburnt areas. Furthermore, given the preference of the Dartford Warbler for low shrubby habitats, we also predict (2) a faster increase in the abundance of this species than in that of the Sardinian Warbler. Second, if regional population trends do affect the post-fire dynamics of the species, we hypothesise (3) that changes in bird abundance in burnt areas are associated with population trends in areas which have not been affected by fire. According to regional trends, we predict that in unburnt areas, the Dartford Warbler should show a decreasing abundance, whereas the Sardinian Warbler should show a stable or increasing population, which, if this second scenario is valid, should be related to their dynamics in burnt areas.

METHODS

Study area

This study was carried out in the Garraf Natural Park (41º 15’ N, 1º 55’ E), situated 20 km to the south of the city of Barcelona, Spain (NE Iberian Peninsula). The vegetation in this park is dominated by shrubs such as *Quercus coccifera, Pistacia lentiscus, Phillyrea latifolia, Olea europaea, Rosmarinus officinalis* and *Chamaerops humilis,* and by pines (*Pinus halepensis*) in areas which have not been burnt recently. After a long period in which there were only some small fires, two large wildfires have profoundly marked the last two decades. The first burnt 10,000 ha in 1982 and the second, which burnt entirely within the zone previously burnt in 1982, affected 5,000 ha in 1994. The 1994 fire was intensive and the total area covered by the remnant patches of unburnt vegetation accounted for less than 2% of the 5000 ha.

We did not find significant differences in relief and landscape structure between the zone burnt in 1994 and the zone not affected by this fire (Table 1). Moreover, the lithology (Mesozoic calcareous rocks) and phytosociologic composition (*Oleo-Ceratonion* with some plants of *Quercion ilicis* (Folch 1986)) was highly homogeneous. Therefore, we considered the zone that did not burnt in 1994 as a suitable area for controlling the variations of Sardinian and Dartford Warbler populations unrelated to the occurrence of fire. To simplify the terminology of the study sites, hereafter the two zones are called burnt zone and control zone respectively.

Table 1. Similarities in relief (altitude, slope and orientation) and landscape structure (percentage of habitat burnt in 1994 within the zone affected by that fire, and percentage of habitat burnt in 1982 within the zone only affected by that fire) between study zones. Data comes from the comparison of 30 surveys (12.5 ha) randomly distributed in each zone. Mean (SD) and t-test for independent samples are shown for parametric variables, but for orientation, a circular variable, mean angle (angular deviation) and the Watson-Williams test are shown (Zar 1984).

	Burnt in 1982 and 1994	Burnt only in 1982	Test	P
Altitude (m)	333 (101)	376 (104)	t = - 1.62	0.111
Slope (degrees)	14.1º (8.8º)	17.0º (8.4º)	t = - 1.28	0.207
Orientation (degrees)	-24º (63º)	-33º (72º)	$F_{1,53}$ = 0.12	0.265
Habitat (%)	95.6 (8.28)	95.4 (7.03)	t = 1.26	0.900

Bird counting

The censuses were carried out in the burnt zone and the control zone during the breeding seasons of 1995, 1997, 1998 and 2000. We selected 35 stations (19 in the burnt zone and 16 in the control zone), which were located a minimum of 400-m apart to minimise pseudo-replication. Thus a total of 140 censuses was carried out during study period. We also ensured that the area around each station was homogeneous and did not include farmland, urbanised areas or cliffs.

Point-counts were used to assess the abundance of the Sardinian Warbler and the Dartford Warbler (Bibby *et al*. 1992). We conducted censuses with several counting bands to analyse the differences in detectability between the two species (Bibby *et al.* 1992). Although detectability sharply decreased in the farthest bands (at more than 50 m from the observer) for both species, the detectability curve in relation to distance did not differ significantly between the two species (χ^2_3 = 1.036, P = 0.207 for the control zone and χ^2_3 = 2.731, P = 0.565 for the burnt zone). Therefore, to maximise the number of contacts per census station, we decided to obtain abundance estimates by means of point-counts to infinity, that is, counting all birds seen or heard at any distance from the observer. Thus, from here onwards, abundance means number of individuals detected per counting station.

Counting was conducted in the morning, during the hours of maximum bird activity, and started 1 h after dawn and 5 min after the arrival at the station. Point-counts taken by other authors have ranged from 5 to 20 min, but following the recommendations made by Fuller and Langslow (1984), 10 min was chosen as a compromise. Whenever we were sure that we had already observed the same individual it was not included as a new record. We carried out bird censuses exclusively under uniformly good weather, without rainfall or wind.

Data analysis

We used repeated measures ANOVA and the post-hoc Tukey Honest Significant Difference (HSD) test to analyse temporal variations in the abundance of the two species throughout the study period in both the burnt and the control zones (Sokal & Rohlf 1995). All statistical analyses were run with Statistica Statsoft, Inc 1999.

RESULTS

We found a continuous increase in overall abundance of the warblers in the burnt zone after the occurrence of fire ($F_{3,72} = 22.83$, $P < 0.001$), but the speed of re-colonisation differed between the two species since the interaction between time since fire and the abundance of the two species was significant ($F_{3,72} = 4.00$, $P < 0.05$). The results of the Tukey HSD test showed that the abundance of both species did not differ until de forth year after fire; however, the Dartford Warbler became significantly more abundant than the Sardinian Warbler from then on (Fig. 1). Therefore, the two species colonised the burnt zone at a similar speed until the fourth year after fire, when the population of the Dartford Warbler began to increase faster.

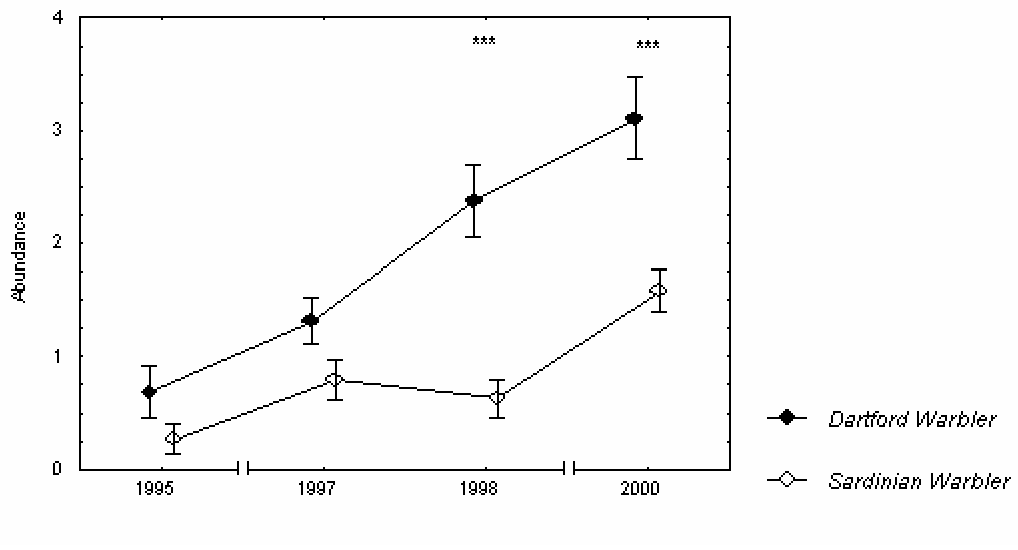

Figure 1. Variation in the abundance (measured as number of individuals detected in a station during the 10-minute census) of the Dartford Warbler and Sardinian Warbler in the burnt zone. Bars indicate Standard Error. Significant differences between zones in a year, according to Tukey HSD test are marked *** at the top of the figure.

Regarding the whole study period, the overall abundance of the Dartford Warbler did not differ between the burnt and the control zone ($F_{1,33}$ = 0.179, P = 0.674). Nevertheless, the abundance of this warbler increased significantly from 1995 to 2000 ($F_{3,99}$ = 5.570, P < 0.01). This trend was highly influenced by the zone ($F_{3,99}$ = 7.488, P < 0.001) since although the abundance of this species remained constant in the control zone, it steadily increased in the burnt zone (Fig. 2). The results of the Tukey HSD test showed that the abundance of the Dartford Warbler was significantly lower in the burnt zone than in the control zone in 1995 and 1997, did not differ in 1998 and was significantly higher in the burnt zone in 2000 (Fig 2). In summary, the temporal pattern shown by the Dartford Warbler in the burnt zone was characterised by a continuous increase in abundance, reaching even higher values than those measured in the control zone.

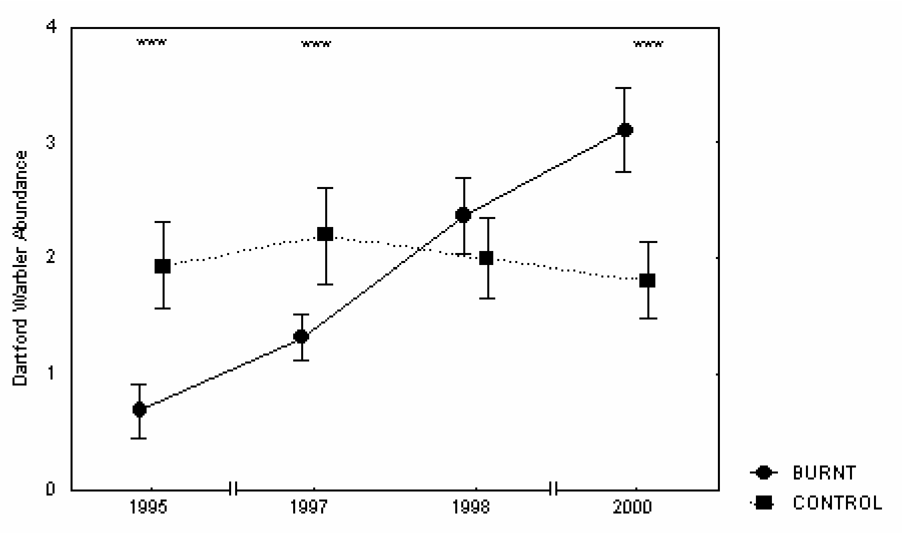

Figure 2. Variation in the abundance of the Dartford Warbler (measured as number of individuals detected in a station during the 10-minute census) after the 1994 fire in the two study areas. Bars indicate Standard Error. Significant differences between zones in a year, according to Tukey HSD test are marked *** at the top of the figure.

The populations of Sardinian Warblers differed between zones ($F_{1,33}$ = 17.347, P < 0.001) and between years ($F_{3,99}$ = 12.120, P < 0.001). These temporal variations were consistent between zones and the interaction between zones and years was not significant ($F_{3,99}$ = 0.580, P = 0.981) (Fig. 3). Therefore, although the abundance of the Sardinian Warbler was always significantly lower in the burnt than in the control zone (see results of Tukey HSD test in Fig. 3), the pattern of variation was the same in both zones.

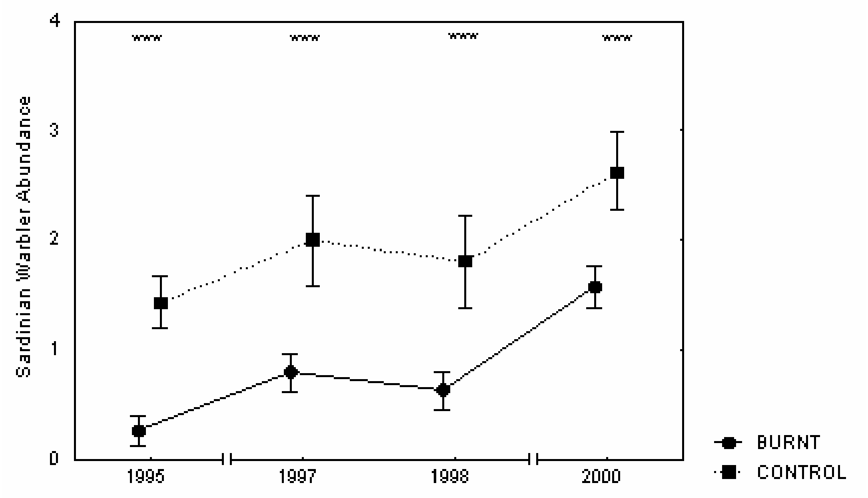

Figure 3. Variation in the abundance of the Sardinian Warbler (measured as number of individuals detected in a station during the 10-minute census) after the 1994 fire in the two study areas. Bars indicate Standard Error. Significant differences between zones in a year, according to Tukey HSD test are marked *** at the top of the figure.

DISCUSSION

Our results showed that Dartford and Sardinian Warblers occurred at low densities in the burnt zone from the first year after fire. These two warblers cannot usually breed the first year after a severe fire (Prodon & Lebreton 1983, Prodon *et al.* 1987, López & Guitian 1988, Llimona *et al.* 1993), but Martin (1983), Pons and Prodon (1996) and Pons (1998) reported their occurrence the first breeding season after fire. This was explained by the presence of remnant patches of unburnt vegetation within the burnt zone. In our burnt zone, as in the case of Pons and Prodon (1996), less than 2% of surface covered by unburnt vegetation appears to be enough for the persistence of both species.

Our results allow the comparison between the abundance of the two species because we did not find differences in their detectability in any of the study zones (see methods). In the burnt zone, the abundance of the two species did not differ significantly until the fourth breeding season after fire, and hereafter the population of the Dartford Warbler increased faster than that of the other species. Therefore, we did not observe that the population of this species, which has a greater preference for low bushes (Cody & Walter 1976, Martin & Thibault 1996), increased faster than the other during the first years following fire, but it did increase from the fourth year onwards. We suggest that this pattern reflect that this species depend on remnants of unburnt shrubs at initial stages, but it rapidly colonises the burnt surroundings as soon as the sprouting shrubs have grown enough. However, the Sardinian Warbler seemed unable to colonise the sprouting shrubs and its population did not increase in a similar way to that of the Dartford Warbler.

Six years after fire, the Dartford Warbler reached higher densities in the burnt zone than in the control. Pons (1998) reported a similar pattern for this species in prescribed burnt shrublands of southern France. He found that the variations in Dartford Warbler abundance were closely related to the change in vegetation cover throughout succession, surpassing pre-fire densities in the fourth breeding season after fire, that is to say, two years sooner than in our drier study zone. The sharp increase of Dartford

Warbler numbers in the burnt zone contrasted with their stability in the control zone, which does not confirm, at this geographical and temporal scale, the regional decline suggested by Tucker and Heath (1994). Our data suggest that Dartford Warbler population trends in the burnt zone are locally driven by habitat changes that are associated with post-fire dynamics. Rabenold *et al.* (1998) also reported that bird dynamics in disturbed habitats were inconsistent with regional population trends. However, when the same type of local habitat changes appear repeatedly here and there, the sum of local population trends can finally modify the temporal trends of birds on a larger scale (Holmes 1988, Virkkala 1991). In this respect, burnt areas (which are common in the Mediterranean, and have highly variable spatial and temporal occurrence patterns) can influence regional population trends. Because the abundance of the species varies rapidly with time since fire, modelling regional population trends in relation to fire distribution and frequency is difficult. It could, however, be relevant for the accurate monitoring of regional population trends of a species catalogued as vulnerable (Tucker & Heath 1994).

In accordance with its preference for medium and tall bushes (Cody & Walter 1976, Martin & Thibault 1996), the Sardinian Warbler showed a lower abundance in the burnt zone than in the control zone throughout the study. Herrando & Brotons (in press) actually showed that Sardinian Warbler juveniles from the burnt zone have lower body condition (estimated by means of fluctuating asymmetry) than those living in the control zone, suggesting that burnt zones are of overall lower quality for this species. The progressive increase of Sardinian Warblers in both zones might be solely related to an enhancement of habitat quality resulting from post-fire dynamics, since the control zone was, in fact, also burnt in 1982. However, censuses conducted in 1997 and 1998 in a nearby area, which have not burnt for the last 50 years, showed no significant differences between the abundance of Sardinian Warbler in this area and that in the control zone (Herrando unpubl.), suggesting that the increase in the control zone is not associated with post-fire dynamics. Therefore, our results indicate that, independently of the occurrence of fire, this species increased its density throughout the study area, which suggests a regional increase for this species. Tucker & Heath (1994) considered that the population of Sardinian Warblers was stable in Europe, whereas Pérez de Ana (1993) found the species to be expanding its geographical distribution in the Iberian Peninsula. Similar trends have been suggested elsewhere (Andryushchenko *et al.* 1993, Hofmans 1998). This general pattern of increase is probably a result of more favourable climatic conditions during the last decade, which was characterised by mild winters (Pérez de Ana 1993). But more interestingly, this increase in the abundance of Sardinian Warblers was parallel in the two study zones, suggesting that the temporal changes in the abundance of this species in the burnt zone are, to some extent, unrelated to the occurrence of fire and the consequent recovery of vegetation but rather related to population trends occurring at a larger scale.

In conclusion, our results fitted our first hypothesis for the Dartford Warbler, since habitat recovery had a strong effect on its post-fire dynamics. In contrast, the Sardinian Warbler fitted our second possible scenario, which suggested that population trend on a larger scale than the local disturbed habitat could be involved in the post-fire dynamics of burnt areas. These results highlight that bird community succession is an assembly of responses of independent species to a variable number of environmental factors that reach further than simple changes in the local habitat.

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Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? [1]

Abstract

Large burnt areas have increased considerably in southern Europe. Knowledge of bird species response is required to design management plans to prevent large wildfires and to preserve biodiversity at the same time. We investigated the spatial variability of both avifauna and habitat structure in three zones: unburnt, burnt in 1982 and burnt in 1994. The habitat structure of the unburnt zone was the most spatially variable but its bird community was very homogeneous in space. In contrast, the bird communities inhabiting burnt zones were highly heterogeneous in space. This pattern was caused by distinct specific responses to variations in habitat structure. Open space species responded to small changes in habitat structure with large changes in local abundance, whereas the response of forest species to these structural variations was much lower. We suggest that managers should select specific zones with limited vegetation recovery within large burnt areas and maintain them as open space to keep combustibility low and provide an appropriate habitat for some open space species that are under conservation concern.

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[1] With Lluís Brotons and Santiago Llacuna. University of Barcelona. Submitted

INTRODUCTION

Humans have been sculptors of Mediterranean landscapes for so long that di Castri (1981) considered that a complex “co-evolution” has shaped the interactions between them and ecosystems. During this long-lasting common history, an amount of activities such as cultivation, irrigation, livestock grazing, cutting and burning have yielded the typical mosaic of Mediterranean landscapes. Nevertheless, the widespread abandonment of traditional land use in most Euro-Mediterranean regions during the 20th century has lead to the growth of extensive and continuous forest and shrubby areas that are very susceptible to large fires (Blondel & Aronson 1999). Fires can increase landscape heterogeneity by fragmenting continuous blocks of older forests and by originating small scale perturbations leading to younger successional stages, but sometimes, fires are so extensive and severe that they reduce structural diversity and homogenise landscape at a regional scale (Trabaud & Galtié 1996, Chuvieco 1999). In the case of Mediterranean countries and as a result of fire propagation in abandoned lands, a new landscape characterised by huge areas (thousands of hectares) covered by shrublands coexisting with patches of unburnt forests, has rapidly spread in recent decades. Present day management policies aimed at preventing large wildfires are focussing on landscape planning as a way to fight against fire. Such policies favour the creation of open areas with low amount of combustible, which are able to stop the violent progression of wildfires and thus facilitate their extinction (Hardy & Arno 1996).

The effects of habitat changes derived from landscape management on birds have been little studied in the Mediterranean Basin (but see: Díaz & Martin 1998, Díaz *et al.* 1998, Pons 1998). So far, the effects of fires on Mediterranean bird communities have mostly dealt with the bird species turnover and its close association with the changes in vegetation following post-fire dynamics (Lawrence 1966, Prodon *et al.*1984, Stanton 1986, Prodon *et al.* 1987, Pons & Prodon 1996, Izhaki & Adar 1997). However, no studies have directly focussed on the spatial variations of bird communities inhabiting extensive shrubby habitats originated in post-fire dynamics.

The main objective of this study was to determine the consequences of large fires on the spatial variability of bird communities. Specifically, we would like to answer these questions: does spatial variability of bird communities differ between burnt and unburnt zones? What is the association between habitat structure and variability of bird communities? Do species that inhabit burnt and unburnt zones respond similarly to small changes in habitat structure?

Effects of large fires on biodiversity are recently receiving much concern because they seem to be a major threat to a number of European bird species (Rocamora 1997). Therefore, this study also attempts to derive guidelines aimed at combining protection of interesting Mediterranean bird species and large fire prevention.

METHODS

Study area

This study was carried out in the Garraf Natural Park, situated 20 km to the south of the city of Barcelona (NE Iberian Peninsula). The study area (41º 15’ N, 1º 55’ E) consists of low hills and small valleys located between 100 and 500 m.a.s.l. Yearly average precipitation ranges from 450 to 650 mm, but the karstic lithology of these hills provides only skeletic soils which implies very dry conditions for plant communities. Until now, most of the works about the effects of fire on bird communities conducted in the Mediterranean basin have been carried out in areas with acid soils and/or relatively high rainfall. In contrast, our study was performed in a dry and karstic landscape and thus it represents a new contribution to the knowledge of avian dynamics after fire in this type of ecosystems.

The studied area was intensively farmed until the end of nineteenth century, when the *Phylloxera* crisis ruined the vineyards that occupied the slopes of the hills almost entirely. Then it began a sudden episode of rural depopulation and its consequent land abandonment. This episode was characterised by the constant growth of natural formations, only slightly affected by fires. Thus, secondary forests of Aleppo pine *Pinus halepensis* progressively covered large areas. Traditionally, these forests have been subject to distinct management practices such us cutting the tallest pines and limiting the cover of shrubs to reduce competition with trees (Vélez 1990). Two extensive fires profoundly marked the latest decades: the first burnt 10,000 ha in 1982 and the second, which burnt over the first, affected 5,000 ha in 1994. The north and west of the Park has not been damaged by fire in recent years and here the pines were present everywhere, even in sites where soil is very thin. Hereafter these zones will be also called F82, F94 and the unburnt zone respectively. Therefore, this area provided an appropriate framework to study the bird communities that inhabit dry Mediterranean landscapes affected by large fires.

Bird Counting

The censuses were carried out during the breeding season (between March and June) of 1997. The bird-count method was employed to assess the abundance of bird species. It is also accepted as a suitable way to relate bird abundance to habitat features (Bibby *et al*. 1992). We select 30 counting stations at each of the three zones (F94, F82 and the unburnt zone), locating them at a minimum 400-m distance from each other to avoid pseudoreplication. We also assured that the area around each station did not include farmland, urbanised areas or cliffs. As the bird censuses were conducted twice, we carried out a total of 180 replicates.

Counting was conducted in the morning, during the period of maximum activity for birds, starting 1 h after dawn, 5 min after the arrival at the station. Point counts taken by other authors have ranged from 5 to 20 min, but following the recommendations of Fuller and Langslow (1984), 10 min was chosen as a compromise. All birds heard or seen were allocated in several circular bands around the observer but in this work we used all records detected within an unlimited radius since the main interest of this study was obtaining relative abundance indices comparable between counting stations. Abundance indices were obtained for each species by selecting the maximum number of individuals detected in any of the two counts at each station. Raptors, aerial feeders (swallows, swifts, bee-eaters,...) and crepuscular species were not taken into account in the calculations because this method is not appropriate for assessing their abundance (Bibby *et al*. 1992). We censused birds exclusively under uniformly good weather conditions, without rainfall or wind. Bird censuses were performed by the same observer in order to avoid interpersonal errors.

The number of species or richness was the only direct index used in the posterior analysis. Classical measurements of diversity such as Shannon index H’ were not used because they are positively correlated with richness and the supplementary information conveyed by H’ is low. This is largely due to the relative high equitability of the breeding bird communities (Prodon 1992).

Vegetation sampling

As habitat characteristics has been repeatedly reported to play a determinant role in structuring bird communities (McArthur & McArthur 1961, Wilson 1974, Wiens 1989), we surveyed the vegetation structure at each bird-count station, following the methodology explained by Prodon and Lebreton (1981). We estimated the cover of distinct vegetation layers (0-0.25 m, 0.25-0.5 m, 0.50-1 m, 1-2 m, 2-4m, 4-8m, 8-16 m) and rock layer as habitat variables in an area that covers approximately 1 ha around the observer. (The few values above zero in the 16-32 m layer were not taken into account in the calculations). Within each layer, the relative cover value was defined as the projection of the foliage volume of the layer (or rock layer) onto a horizontal plane. We estimated this projection by comparison with the reference chart according to Prodon and Lebreton's procedure (1981). According to these authors, this method allows the observer to reach a reliability of ±10 %. Cover variables were estimated by the same observer in order to avoid interpersonal errors.

Statistical analyses

We performed an analysis of variance and a Tukey honest significant difference (HSD) test for post hoc comparisons to analyse differences in average richness among zones (Sokal & Rohlf 1995).

Correspondence analysis is a descriptive/exploratory technique designed to analyse multi-way tables containing some measure of correspondence between the rows and columns (Greenacre 1984). This type of analysis is especially interesting in the study of relationships between birds and habitats due to its property of optimisation and to the symmetrical role played by the species and the sample stations. Correspondence analysis attributes scores both to species and to stations so that the correlation between station scores and species scores is maximal, given the best "correspondence" between species and stations (Prodon 1992). This method allowed us to visualise the degree of aggregation of stations belonging to the three zones studied (F94, F82 and the unburnt) in the factorial space. The stations more grouped correspond to those that tend to have the same bird community and the more scattered are those with less spatial homogeneity. The variance of species scores for a given zone was used as a measure of the spatial variation of bird communities within this zone. We performed another correspondence analysis for vegetation structure that avoid the intercorrelation and the number of these variables as well as to determine the important features of habitat structure. Differences in the variability of scores for each factor between zones were tested by means of a Barlett Chi-square test (Sokal & Rohlf 1995).

In order to find out relationships between bird species and habitat structure variables we employed generalised linear models (McCulagh & Nelder l983). For each species, we used its relative abundance as dependent variable. All abundances followed a Poisson distribution, except for Sardinian Warbler *Sylvia melanocephala*, which abundance fitted a normal distribution. Therefore, we used different error distributions in each specific model according to the characteristics of the dependent variable. A backward step-wise procedure (*P* to enter=0.05, *P* to remove=0.10) was conducted to select only significant factors from the initial set of predictors that included the first two factors of the correspondence analyses carried out with the variables used to describe the habitat features. For each significant association between the abundance of a bird species and any structural factor we determined the sign of the relationship (positive or negative), and the estimate of the relationship, that is to say the degree of change in the dependent variable produced by changes in the independent one(s). All statistical analyses were run with Statistica Statsoft, Inc 1999.

RESULTS

Bird species richness

A total of 36 bird species were recorded during the breeding season: 19 of them in F94, 23 in F82 and 25 in the unburnt zone (Table 1). The average richness per station was 6.0 (*SD*=1.8) in F94, 5.6 (*SD*=2.9) in F82 and 11.7 (*SD*=2.9) in the unburnt zone, and it differed significantly between the three zones ($F_{2,58}$=58.78, *P*<0.0001). The post hoc comparisons of means performed with the Tukey HSD test showed that the unburnt zone showed higher average richness per station than any of the burnt zones (*P*<0.0001 in both cases), but this parameter did not varied between F82 and F94 (*P*=0.87).

Table 1. List of the bird species found in the three studied zones: F94, F82 and the unburnt zone (u). The scores of the first two factors (F1 and F2) of the correspondence analysis for each bird species are also shown.

Bird species		Zone	F1	F2
Robin	*Erithacus rubecula*	u	1.024	0.655
Blue Tit	*Parus caeruleus*	u	0.987	0.618
Short-toed Treecreeper	*Certhia brachydactyla*	u	0.947	0.413
Bonelli’s Warbler	*Phylloscopus bonelli*	u	0.932	0.346
Coal Tit	*Parus ater*	u	0.931	0.452
Crested Tit	*Parus cristatus*	u	0.927	0.377
Wood Pigeon	*Columba palumbus*	u	0.904	0.345
Magpie	*Pica pica*	u	0.894	0.290
Wren	*Troglodytes troglodytes*	F82, u	0.878	0.281
Jay	*Garrulus glandarius*	F82, u	0.875	0.320
Turtle Dove	*Streptopelia turtur*	u	0.854	0.302
Golden Oriole	*Oriolus oriolus*	u	0.839	0.138
Firecrest	*Regulus ignicapillus*	F82, u	0.820	0.193
Long-tailed Tit	*Aegithalos caudatus*	F82, u	0.810	0.129
Nightingale	*Luscinia megarhynchos*	F82, u	0.784	0.145
Common Cuckoo	*Cuculus canorus*	F82, u	0.723	-0.030
Green Woodpecker	*Picus viridis*	F94, u	0.694	0.392
Goldfinch	*Carduelis carduelis*	F94, F82, u	0.510	0.162
Cetti’s Warbler	*Cettia cetti*	F82, u	0.447	-0.139
Great Tit	*Parus major*	F94, F82, u	0.421	-0.218
Blackbird	*Turdus merula*	F94, F82, u	0.399	-0.086
Greenfinch	*Carduelis chloris*	F94, F82, u	0.373	0.018
Rock Bunting	*Emberiza cia*	F94, F82, u	0.299	-1.419
Serin	*Serinus serinus*	F94, F82, u	0.191	-0.055
Sardinian Warbler	*Sylvia melanocephala*	F94, F82, u	0.044	-0.430
Dartford Warbler	*Sylvia undata*	F94, F82	-0.893	-0.698
Southern Grey Shrike	*Lanius meridionalis*	F94, F82	-1.183	-0.079
Woodchat Shrike	*Lanius senator*	F94	-1.218	1.194
Rock Thrush	*Monticola saxatilis*	F94, F82	-1.244	1.210
Red-legged Partridge	*Alectoris rufa*	F94, F82	-1.257	-0.077
Stonechat	*Saxicola torquata*	F94, F82	-1.291	0.718
Black-eared Wheatear	*Oenanthe hispanica*	F94, F82	-1.329	0.599
Ortolan Bunting	*Emberiza hortulana*	F94, F82	-1.421	1.687
Thekla Lark	*Galerida theklae*	F94, F82	-1.516	0.465
Corn Bunting	*Miliaria calandra*	F94	-1.540	1.593
Tawny Pipit	*Anthus campestris*	F94, F82	-1.708	2.044

Bird community structure

The correspondence analysis of bird data showed that a total of 29.61% of the variance was explained by the first two factors (21.83% for F1 and 7.78% for F2), which was high given the large data matrix (36 species). On the one hand this analysis sorted the bird species according to their abundance at each station. Thus, F1 represents a progressive gradient from birds that are typical of open habitats (negative scores) to forest birds (positive scores) and F2 represents a gradient from birds that usually inhabit shrubby habitats (negative scores) to birds either from open or from woody areas (positive scores) (Table 1). On the other hand the same analysis also showed the ordination of counting stations according to their avifauna. Thus, there was a large overlap between the stations of F94 and those of F82, whereas stations located in burnt zones did not overlapped with those of the unburnt zone (Fig.1). Moreover, although point-counts ordination showed a continuum from burnt to unburnt habitats, the counting stations situated in the unburnt zone were more clumped than the stations belonging to burnt zones. Statistically, the variance of the scores was significantly higher in F94 than in the unburnt zone (Bartlett χ^2=31.04, P<0.0001 for F1 and χ^2=47.94, P<0.0001 for F2) and it was also higher in F82 than in the unburnt zone (Bartlett χ^2=48.76, P<0.0001 for F1 and Bartlett χ^2=38.43, P<0.0001 for F2). In contrast, the variance of the scores of the two burnt zones did not differ, although F82 showed marginally more variance than F94 for F1 (Bartlett χ^2=3.61, P=0.057 for F1 and Bartlett χ^2=1.01, P=0.314 for F2). Therefore, the stations located in the unburnt zone had similar bird communities whereas the counting stations located in burnt zones showed a bird community that was more spatially variable.

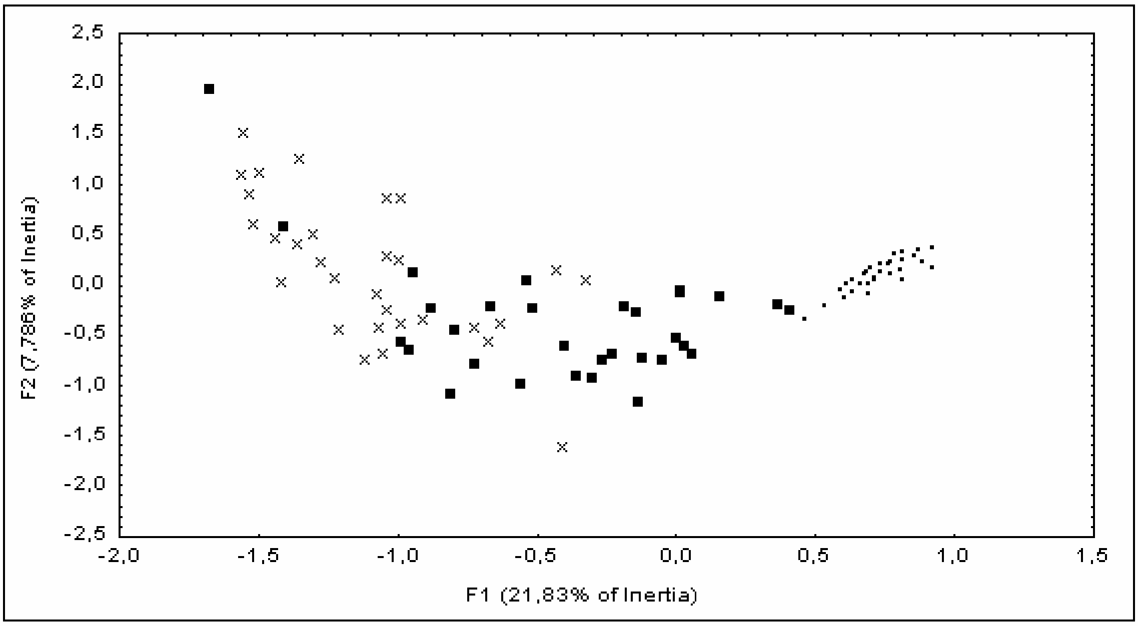

Figure 1. Projection of the 90 bird counting stations on the plane defined by the first two factors (F1 and F2) of the correspondence analysis of breeding bird communities. Crosses mean F94 stations, squares F82 stations and points the unburnt stations.

Habitat structure

The first two factors of the correspondence analysis performed with the structural data accounted for 68.92% of the total data matrix variance (Table 2). The first factor (SF1) was correlated with all the variables, from the most negative (rocks) to the most positive (trees). Therefore, this factor may be interpreted as a gradient of increasing structural complexity, which was closely related to fire influence. The second structural factor (SF2) was positive correlated with large trees and very small plants (herbs or small ligneous plants less than 25 cm tall) and negatively with shrubs from 50 cm to 2 m tall.

Thus, SF2 represented a gradient of shrub development in contrast with tree or small plants development. Shrub layers were not present neither in recently burnt sites nor in many Iberian forest, which are commonly managed to limit the grow of shrubs (López & Moro 1997). An obvious but noticeable point was that F94 had the fewest number of vegetation layers whereas the unburnt zone had the highest. In fact, the unburnt zone showed significant higher variance of structural factors than F94 (Bartlett χ^2=27.36, P<0.0001 for SF1 and Bartlett χ^2=23.86, P<0.0001 for SF2) (Fig. 2). The structural factors were also more variable in F82 than in F94 (Bartlett χ^2=20.92, P<0.0001 for SF1 and Bartlett χ^2=9.09, P=0.006 for SF2). Finally, the unburnt zone showed significant higher variances than F82 in SF2 (Bartlett χ^2=5.78, P=0.016) but not for SF1 (Bartlett χ^2=0.63, P=0.425). Therefore, the spatial variation of structural factors, which is commonly reported to induce variations on bird communities, was higher in the forested than in the more open areas. However, there is an apparent contradiction with the results of the correspondence analysis performed with birds, which showed the highest spatial variability of bird communities in shrubby zones and the fewest the unburnt one.

Table 2. Correlations between the relative cover of each structural layer (vegetation layers and rock layer) and the first two factors of the correspondence analysis carried out with structural data (SF1 and SF2).

	SF1	SF2
Rock %	-0.665***	0.168
0.00-0.25 %	-0.358**	0.713***
0.25-0.50 %	-0.340**	-0.203
0.50-1.00 %	0.577***	-0.734***
1.00-2.00 %	0.701***	-0.431***
2.00-4.00 %	0.698***	-0.131
4.00-8.00 %	0.755***	0.176
8.00-16.00 %	0.664***	0.425***
% Variation explained	44.93	23.99

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

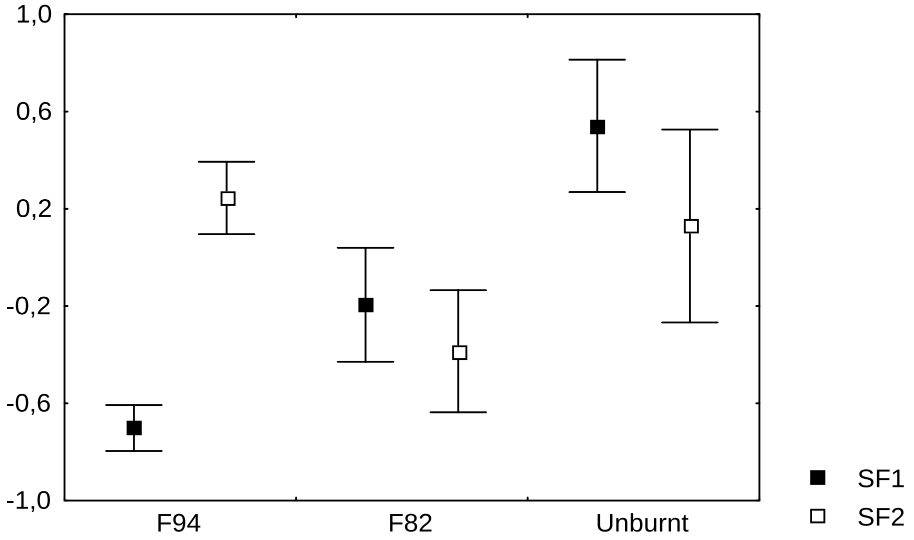

Figure 2. Mean and standard deviation for structural factors (SF1 and SF2) in F94, F82 and the unburnt zone. Solid squares indicate SF1 and open squares indicate SF2.

Birds-habitat structure relationship

The first factor of the correspondence analysis performed with birds (F1), which was interpreted as a gradient from birds of open habitats to birds of woody habitats according to the ecology of the species, was actually positively correlated with the SF1 (r=0.87, P<0.0001). Similarly, F2 was positively correlated with SF2 (r=0.52, P<0.0001). These results support the previous interpretation of the first two factors (F1 and F2) of the bird correspondence analysis.

We used generalised linear models to determine what kind of relationship was behind the bird response to changes in habitat features (Table 3).

Table 3. Generalised linear models using the abundance of each bird species as dependent variable. A backward step-wise procedure (P to enter=0.05, P to remove=0.10) was conducted to select only significant factors from the initial set of predictors that included the two main factors of the correspondence analyses performed with structural variables (SF1 and SF2). All dependent variables followed a Poisson distribution, except for Sardinian warbler which abundance fitted a normal distribution. Species are ordered according to F1 scores.

Species		Intercept	SF1	SF2	χ^2	d.f.	*P*
Robin	*Erithacus rubecula*	-4.28**	1.55^a		4.95	1	0.025
Short-toed Treecreeper	*Certhia brachydactyla*	-2.07***	2.36***		37.80	1	<0.0001
Bonelli’s Warbler	*Phylloscopus bonelli*	-1.99***	1.68***		23.08	1	<0.0001
Coal Tit	*Parus ater*	-3.11***	2.15**		10.49	1	<0.0001
Crested Tit	*Parus cristatus*	-1.73***	2.17***		36.14	1	<0.0001
Wood Pigeon	*Columba palumbus*	-1.74***	2.07***		44.34	1	<0.0001
Magpie	*Pica pica*	-3.04***	1.81**		12.39	1	<0.0001
Wren	*Troglodytes troglodytes*	-0.38*	1.73***		86.22	1	<0.0001
Jay	*Garrulus glandarius*	-2.02***	2.02***		28.21	1	<0.0001
Turtle Dove	*Streptopelia turtur*	1.78***	1.56***		20.22	1	<0.0001
Golden Oriole	*Oriolus oriolus*	-2.40***	1.74**		16.33	1	<0.0001
Firecrest	*Regulus ignicapillus*	-1.66***	1.58***		19.08	1	<0.0001
Long-tailed Tit	*Aegithalos caudatus*	-1.68***	1.87***		26.96	1	<0.0001
Nightingale	*Luscinia megarhynchos*	-1.04***	1.30***		22.44	1	<0.0001
Common Cuckoo	*Cuculus canorus*	-1.81***	1.12**		8.65	1	0.003
Green Woodpecker	*Picus viridis*	-2.07***	2.38**	1.49**	21.35	2	<0.0001
Blackbird	*Turdus merula*	-0.24***	1.05***		26.03	1	<0.0001
Great Tit	*Parus major*	-0.45**	1.22***		28.98	1	<0.0001
Greenfinch	*Carduelis chloris*	-1.81***	1.12**		8.65	1	0.003
Serin	*Serinus serinus*	-0.305*	0.73***		13.86	1	<0.0001
Sardinian Warbler	*Sylvia melanocephala*	0.80***	0.41***	-0.54**	32.41	2	<0.0001
Dartford Warbler	*Sylvia undata*	-0.94**	-3.25***	-2.56*	111.02	2	<0.0001
Southern Grey Shrike	*Lanius meridionalis*	-2.06***	-2.65**		17.68	1	<0.0001
Woodchat Shrike	*Lanius senator*	-4.70**	-3.02*		9.55	1	0.002
Red-legged Partridge	*Alectoris rufa*	-1.99***	-3.26**		40.43	1	<0.0001
Stonechat	*Saxicola torquata*	-1.61***	-2.62***	-0.67a	35.79	2	<0.0001
Black-eared Wheatear	*Oenanthe hispanica*	-2.14***	-3.64***		59.20	1	<0.0001
Thekla Lark	*Galerida theklae*	-3.56**	-2.73**		4.71	1	0.029
Corn Bunting	*Miliaria calandra*	-6.20*	-5.36*		17.89	1	0.002
Tawny Pipit	*Anthus campestris*	-5.97**	-4.47*	5.19*	25.18	2	<0.0001

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ^{a} $P < 0.1$.

Out of the 36 bird species found in the study, 30 had a model which included SF1, whereas SF2 was only included in the model of five species. A positive relationship between abundance and a gradient of increasing structural complexity (SF1) was found in 21 species, whereas only in nine species was abundance negatively related to SF1. The estimate of each relationship is the slope of the equation, and thus, a high estimate implies a high variation in species abundance due to a fixed variation in the structural factor. For the set of species positively related to SF1, the mean absolute estimate (which was 1.60) was significantly lower (t_{28}=-6.95, P<0.0001) than that of the set of the species that were negatively related to SF1 (which was 3.44). Therefore, small variations in the first component of habitat structure induced greater effects in the abundance of species negatively associated with this structural factor than in the abundance of the species positively associated.

DISCUSSION

Our results showed that the bird species inhabiting the unburnt Aleppo pine forests differed notably from those of the zones affected by fire, whereas the bird species of the two burnt zones, burnt by last time either in 1982 or in 1994, were quite similar. Therefore, although we can not reconstruct directly a successional process with these three zones burnt at distinct times (Prodon & Pons 1993), there is enough evidence of the slow succession towards the forest communities. It contrasts with other studies carried out in Atlantic Iberian ecosystems (López & Guitian 1988, García 1997) or even in other more humid Mediterranean ecosystems (Prodon *et al.* 1987, Vicente 1991, Prodon 1992, García 1997), where the vegetation succession was clearly faster. This pattern is linked with the slowness in the recovery of the plant community in dry conditions.

Helle and Mönkkonen (1990) suggested that, for many types of ecosystems, the relative growth rate of vegetation often reaches its peak during the intermediate stages of forest succession and it is associated with a rapid change in bird communities. In Mediterranean landscapes, Prodon (1992) showed that in the transition between shrubland and forest stages any variation in the tree/shrub ratio was sufficient to induce noticeable changes in the avifauna composition associated with a rapid increase in bird diversity. According to this author, it may be caused by the presence of patchy vegetation at this stage, when bushes and scattered young trees coexist for several years before canopy closure. These transitions are composed of assemblages of forest and open landscape bird species resulting from a deficit of species specific of intermediate successional stages. Most of the F82 stations had a bird community formed basically by species typical of shrubby habitats with few forest species. Therefore, 15 years after fire, the bird community of the studied area had not achieved the transitional stage reported by Prodon (1992), although a few stations showed a bird community which was close to the unburnt ones. According to the habitat structure of these stations, this period of rapid turnover may coincide with the moment when trees reach 4 or 5 m tall.

At a regional level, Blondel and Farré (1988) showed that forest bird communities were very similar in distinct European areas, whereas those of open habitats differed significantly. These authors pointed out that open or semi-open habitats were more directly subjected to local environmental factors than forests, which conditions were largely buffered by the habitat structure. Our results show a comparable pattern at a smaller scale. In fact, the bird communities inhabiting the unburnt forested zone were more spatially uniform than those inhabiting open or semi-open burnt zones. Structural changes in this Mediterranean forest provoked few variations in the rather constant bird community. In contrast, the bird communities inhabiting zones affected by fire were largely determined by small changes in habitat structure. Within the two zones disturbed by fire, burnt either 15 or three years before the field work, the bird communities inhabiting the former were the most variable in space. As mentioned before, this zone contained some stations with young trees sticking out up to 5 m from a dense and tall shrub layer and thus contained a bird community quite similar to the unburnt. Nevertheless, in other F82 stations vegetation was mainly lower than 50 cm tall and only punctually some Aleppo pines exceeds this height without reaching more than 1.5 m tall. These notable differences in vegetation development may be in direct association with soil deep. Soil heterogeneity may be also found in the zone burnt in 1994 but here the time elapsed since fire had not been enough to allow the growth of vegetation in sites with adequate soil conditions. Therefore, our results suggest that fire increase the spatial variability of bird communities but to a greater degree in areas burnt more than ten years before than in areas recently burnt.

The variability of habitat structure showed a pattern that was opposite from the pattern showed by bird communities. In fact, the habitat structure was spatially variable the most in the unburnt zone. This was very likely caused mainly by two factors: a greater variability intrinsic to a system with more vegetation layers and the presence of forest management practices carried out with different intensity. However this variability did not induce almost any change in the bird community. Thus, the mere presence of Aleppo pines implied the appearance of forest bird communities, which were highly shaped by the presence of these trees but were not much influenced by the variability within the forest vegetation layers, at least compared with the post-fire communities. López and Moro (1997) found that the composition of bird communities in Aleppo pine forests of south-eastern Spain was better explained by understorey characteristics than by the tree layer. Even taken in consideration that unburnt stations differed among them in the intensity of tree and understorey management, our results showed that changes in habitat structure affected to a lower degree the bird assemblages of these forests than those of the zones affected by fire.

We found that the bird species living in burnt zones had a response to changes in habitat structure significantly higher than forest species. These results indicate that forest birds were very resilient to the changes of habitat features whereas birds inhabiting burnt zones were highly shaped by small variations in the few layers present in shrubby vegetation. This is why the small variations in the habitat structure of burnt zones lead to large variations in its bird communities, whereas the high degree of spatial variability in forests structure hardly influenced bird communities.

Management considerations for bird conservation

Due to its geographic location, topographic and geographic diversity and traditional human land uses, the Mediterranean region is a ‘hot-spot’ of bird species diversity (Covas & Blondel 1998). However, some studies carried out in European Mediterranean countries have shown a significant reduction in local bird richness as a consequence of land abandonment and the disappearance of open habitats associated with the expansion of woodland (Preiss *et al.* 1997, Farina 1997, Pino *et al.* 2000). In parallel, land abandonment also favoured large fires, especially in dry areas, where sporadic but adverse meteorological situations make fire extinction very difficult (Blondel & Aronson 1999). This work show that large fires have different effects on bird diversity depending on the scale considered. We found more bird species in unburnt stations than in those of the burnt zones, either in 1982 or in 1994. Thus, at this small scale, large fires may be seen as harmful for forest bird diversity. However, the variability of bird communities among the unburnt stations was much lower than it was among the stations of F94 or F82 and, as consequence, bird total richness was not so low in burnt zones. In fact, F82 as a whole zone even had almost as many bird species as the unburnt zone. Therefore, these results emphasise the relevance of the multi-scale approach, which has acquired a great importance among ecologist in recent years (Wiens 1994, Jokimaki & Hutha 1996, Drapeau *et al.* 2000).

Burnt zones have been reported as interesting areas in terms of overall biodiversity conservation (Blondel & Aronson 1999). Only four of the species that inhabited the unburnt area (16 % of species, Turtle Dove *Streptopelia turtur,* Green Woodpecker *Picus viridis,* Sardinian Warbler *Sylvia melanocephala* and Rock Bunting *Emberiza cia* are considered under Conservation Priority A, B, or C with regards to the particular importance of habitat for their survival (Rocamora 1997). In contrast, 12 species (46 % of breeding species) inhabiting burnt zones (Red-legged Partridge *Alectoris rufa,* Green Woodpecker *Picus viridis,* Thekla Lark *Galerida theklae,* Tawny Pipit *Anthus campestris,* Black-eared Wheatear *Oenanthe hispanica,* Stonechat *Saxicola torquata,* Rock Thrush *Monticola saxatilis,* Dartford Warbler *Sylvia undata,* Sardinian Warbler *Sylvia melanocephala,* Woodchat Shrike *Lanius senator,* Rock Bunting *Emberia cia and* Ortolan Bunting *Emberiza hortulana*) are within this conservation category. These results magnify the biological value of the maintenance of burnt areas in relation to forested areas. Fires in very dry areas, such as the Iberian Mediterranean coast, may turn habitats as appropriate for the maintenance of many priority bird species. Therefore, in spite of the general view of these areas as poor lands with a slow vegetation recovery, they may contribute to support a very threatened part of the overall European bird diversity.

Our results also suggested that, within the burnt areas, bird communities are very distinct from one site to another. Considering that many bird species belonging to Conservation Priority A, B, or C (Rocamora 1997) are those that inhabit burnt zones with very small shrubs, it could be interesting to determine specific zones in order to focus conservation policies. Zones that, even several years after fire, are still dominated by small shrubs are those that offer the best habitat for open space species because they are the most resilient to successional processes, and then may support the populations of these birds for longer. Often these zones are affected by frequent fires and then bird species of interest may be able to remain for decades, but in others cases this natural disturbance is not frequent enough and succession finally proceeds. In this case, management practices should be undertaken with the objective of enhancing bird diversity and maintaining open areas with low amounts of vegetation to avoid the violent progression of large and catastrophic wildfires.

Perhaps one of the easiest ways to control the growth of plants may be prescribed burning. Fire itself, if properly managed is a suitable technique for controlling vegetation development and maintain open spaces and community diversity (Richards *et al.* 1999). Prescribed fire is now a widely used management tool that can help to prevent large-scale catastrophic wildfires (Hardy & Arno 1996, Miller & Urban 2000), which usually have a relatively modest impact on bird communities (Bock & Bock 1983, Petersen & Best 1987, Pons 1998, but see Robertson 2000). In Mediterranean France, Pons (1998) found that, after a prescribed fire that burned 76% of a 8.25 ha plot, high priority bird species such as Tawny Pipit *Anthus campestris* and Wood Lark *Lullula arborea* increased their densities, whereas other interesting bird species such as Sardinian Warbler *Sylvia melanocephala* and Dartford Warbler *Sylvia undata* had enough shrubs to remain after the fire. Our results also show that the abundance of bird species with high priority conservation indices responds strongly to small changes in vegetation structure and these changes happen at a small scale, which approximately coincide with the surface that a prescribed burning should cover in terms of large wildfire prevention and social conscience.

The increase of grazing by means of the reintroduction of large herbivores or livestock husbandry is another strategy that can be used to limit the vegetation growth in burnt areas. In a study conducted in eastern Mediterranean, Neeman *et al.* (1997) suggest that an annual short but heavy grazing is a management option for decreasing vegetation mass. The effects of livestock grazing on bird communities has often been evaluated as negative (Bock & Bock 1999, Fuller & Gough 1999), but one of the few studies carried out on the Mediterranean basin has reported positive effects for maintaining some Priority European bird species (Pulido & Díaz 1992).

Given the double interest in diminishing vegetation biomass for avoiding large wildfires and preserving bird species that inhabit open spaces, it is very important to select carefully the appropriate zones to act on. If the choice is unfortunate, the rapid vegetation recovery may turn both objectives unreachable. Therefore, we recommend to concentrate management actions (prescribed burning, grazing or any other management technique suitable to remove vegetation) in specific burnt zones with limited vegetation growth so that biomass accumulation is minimised, maintaining fire barriers active, and the bird community of open spaces conserved.

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Does fire increase the seasonal variability of bird communities? a case in Mediterranean shrublands[1]

Abstract

Fire, a frequent phenomenon in Mediterranean landscapes, is a major ecological disturbance in terrestrial ecosystems. We hypothesised that the bird communities of burnt areas undergo greater seasonal changes than those inhabiting unburnt ones. Using the point-count method we assessed bird species composition and abundance in three zones (unburnt, burnt in 1982, and burnt in 1994) during the breeding and wintering seasons of 1997 and 1998.

From the breeding to the wintering seasons, burnt zones showed an increase in forest species, whereas the bird community of the unburnt zone remained stable in the gradient open-forest species. Moreover, the seasonal turnover of communities was higher in burnt zones than in the unburnt ones, although this did not imply that the former varied in richness through the year. The pattern of bird abundance in the unburnt zone was similar during the two years studied, in contrast with that of burnt zones, suggesting higher annual cyclicity in resource availability in unburnt areas. These findings suggest that fire increases the seasonal variability of bird communities.

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[1] With Lluís Brotons and Santiago Llacuna. University of Barcelona. Submitted

INTRODUCTION

Fires are a natural component of the dynamics of many ecosystems, and have played a dominant role in the Mediterranean Basin (Blondel & Aronson 1999). The study of the effects of fires on Mediterranean bird communities have mostly dealt with the turnover of avifauna and its close association with the changes in vegetation following post-fire dynamics (Lawrence 1966, Prodon *et al*. 1984, Stanton, 1986, Prodon *et al*. 1987, Pons & Prodon 1996, Izhaki & Adar 1997). Nevertheless, bird communities that are under successional processes, such as those provoked by fire, are subjected to other types of temporal variations besides the species turnover that characterises the succession itself. On the one hand, trends due to stochastic events such as droughts, diseases, variations in nearby "source" population, etc. and, on the other hand, the seasonal changes in species composition and abundance that result from cyclical environmental changes which occur each year (Wiens 1989). Seasonal variations in bird communities in relation to habitat characteristics have been widely studied (e. g. Herrera 1978, Rice *et al*. 1980, Alatalo 1981, Bilcke 1984, Kwok & Corlett 1999). However, few attempts have been made to link the seasonal shifts of bird communities directly with the effects of habitat disturbances (but see Hayes & Samad 1998).

The objective of this study was to determine the consequences of fire on the seasonal variability of bird communities. As mature systems are believed to contain a more stable bird community than recently disturbed habitats (Magalef 1968, Odum 1969), we hypothesised that the bird communities in burnt zones undergo greater seasonal shifts than those in unburnt areas. Specifically, we examined whether the seasonal fluctuations in bird communities differed between three zones: a zone burnt 3 years before the beginning of the study, a zone burnt 15 years before, and an unburnt zone.

METHODS

Study area

This study was carried out in the Garraf Natural Park, situated 20 km to the south of the city of Barcelona (NE Iberian Peninsula). The study area (41º 15' N, 1º 55' E) consists of low hills and small valleys located between 100 and 500 m.a.s.l. Yearly average precipitation ranges from 450 to 650 mm, but the karstic lithology of these hills provides only skeletic soils, which implies very dry conditions for plant communities.

The study area was intensively farmed until the end of the nineteenth century, when the *Phylloxera* crisis ruined the vineyards that occupied the slopes of the hills almost entirely and, as a consequence of land abandonment, afforestation played a major role in changing the landscape. Forests of the Aleppo pine *Pinus halepensis* covered large areas until the latest decades of the twentieth century, when two extensive fires profoundly marked the landscape of the Park. The first fire burnt 10,000 ha in 1982 and the second, which burnt over the first, affected 5,000 ha in 1994. The northern and western areas of the Park have not been damaged by fire in recent years and here the pines were present everywhere, even in sites where soil is very thin. Hereafter these zones will be also called F82, F94 and the unburnt zone respectively. This area provided an appropriate framework in which to study the seasonal variation of bird communities that inhabit dry Mediterranean landscapes affected by large fires.

Bird counting

Field work was carried out during the breeding seasons (between March and June) of 1997 and 1998, and during the wintering seasons (between December and February) of 1997/98 and 1998/99. We repeated the same censuses two consecutive years in order to contrast the seasonal trends observed between years. This was done because bird populations and communities vary from year to year due to a substantial number of sources of variation and, therefore, no single year can be considered as typical or average (Wiens 1989).

The point-count method was used to determine bird species composition and abundance at each counting station. We select 30 counting stations in each of the three zones (F94, F82 and the unburnt zone), but we made sure that the area covered by the census around the station was homogeneous and did not include farmland or cliffs. Although we started the monitoring in 1997 with 90 stations, we finished the field work with only 84 stations because some were reburnt or logged. Bird censuses were conducted twice in each season and thus a total of 710 point-counts were carried out. Counting was conducted in the morning, during the period of maximum bird activity, starting 1 h after dawn, and 5 min after arrival at the station, and each count took 10 min. Point counts taken by other authors have ranged from 5 to 20 min, but following the recommendations of Fuller & Langslow (1984), 10 min was chosen as a compromise.

All birds heard or seen were allocated to several circular bands around the observer (Bibby *et al.* 1992). Raptors, aerial feeders (swallows, swifts, bee-eaters,...) and crepuscular species were not taken into account because this method is inappropriate for a census of these species them (Bibby *et al.* 1992). Field work was carried out exclusively under uniformly good weather conditions, without rainfall or wind.

Richness and abundance were used as descriptors of the bird community. For each station, season and year, richness was calculated by considering the total number of species detected within an unlimited radius from the observer at any of the two replicates performed. However, not all the birds detected were used for estimating bird abundance. To compare bird abundance between seasons it must be considered that the detectability of each species changes throughout the year. Passerine birds are usually more detectable in the breeding season, when their territorial songs make them more conspicuous and as a result they can be detected from further away than in the wintering season (Bibby *et al.* 1992). Therefore, abundance estimates must be taken only within a radius that allows all species to be detected equally in both periods. We estimated the detectability of each species in each season and in each habitat following the methodology of Reynolds *et al.* (1980). Thus, we assessed the appropriate radius for estimating the abundance of birds at each station. Classical measurements of diversity, such as the Shannon index H', were not used because they are positively correlated with richness and the supplementary information conveyed by H' is usually low (Prodon 1992).

Statistical analyses

Correspondence analysis was applied to the matrix of bird species composition and counting stations to detect the main factors influencing bird assemblages. This analysis is a descriptive/exploratory technique designed to analyse multi-way tables containing some measure of correspondence between the rows and columns (Greenacre 1984). This statistical tool attributes scores both to species and to stations so that the correlation between the two is maximal, given the best "correspondence" between species and stations (Prodon 1992). Correspondence analysis avoids the intercorrelation between variables and reduces the number of initial variables to a number of factors which are sorted according to their relative weight in the total data matrix variance. We selected only the number of factors that were unequivocally interpreted.

We used repeated measures ANOVA (Sokal & Rohlf 1995) to compare the seasonal shift in bird community descriptors (richness, abundance and the main factors from correspondence analysis) in each zone (F94, F82 and the unburnt zone). All statistical analyses were run with Statistica Statsoft, Inc 1999.

RESULTS

A total of 44 bird species were observed during the field work, 27 in F94, 34 in F82 and 32 in the unburnt zone. Of the bird species found in F94, 44.4% were all year-residents, whereas this percentage reached 55.9% in F82 and 59.4% in the unburnt zone (Table 1).

Table 1. List of the bird species found in the three study zones (F94, F82 and the unburnt zone). Each value indicates the average between the percentage of stations occupied in 1997 and 1998 and the bar separates the percentage of stations occupied in the breeding season (first number) and that in the wintering season (second number). The scores of the first two factors (F1 and F2) of the correspondence analysis for each bird species are also shown.

Bird species		F94	F82	Unburnt	F1	F2
Red-legged partridge	*Alectoris rufa*	56.5/30	18.5/8.5	0/0	1.30	0.17
Common cuckoo	*Cuculus canorus*	0/0	6.5/0	32/0	-0.82	1.06
Green woodpecker	*Picus viridis*	3/0	0/0	31.5/20	-0.80	0.53
Wood pigeon	*Columba palumbus*	0/0	1.5/1.5	48/16.5	-0.91	0.51
Turtle dove	*Streptopelia turtur*	0/0	1.5/0	25/0	-0.85	0.79
Thekla lark	*Galerida theklae*	15/14	3.5/3	0/0	1.58	0.30
Meadow pipit	*Anthus pratensis*	0/10	0/6.5	0/0	0.88	-3.13
Tawny pipit	*Anthus campestris*	21.5/0	3/0	0/0	2.13	1.76
Wren	*Troglodytes troglodytes*	0/17	20/40	88.5/73.5	-0.54	-0.08
Hedge sparrow	*Prunella modularis*	0/19	0/6.5	0/7	0.51	-1.64
Robin	*Erithacus rubecula*	0/65	0/72	10/91.5	-0.09	-0.93
Nightingale	*Luscinia megarhynchos*	0/0	15/0	58.5/0	-0.78	0.78
Black redstart	*Phoenicurus ochrurus*	0/24	0/0	0/0	0.73	-1.75
Stonechat	*Saxicola torquata*	61.5/34	41.5/5	0/0	1.37	0.34
Black-eared wheatear	*Oenanthe hispanica*	80/0	23.5/0	0/0	1.58	0.90
Rock thrush	*Monticola saxatilis*	3.5/0	5/0	0/0	1.31	1.28
Blackbird	*Turdus merula*	26.5/20	60/55	83/86.5	-0.22	-0.07
Cetti’s warbler	*Cettia cetti*	0/0	6.5/3	5/7	-0.67	0.31
Dartford warbler	*Sylvia undata*	97/100	91.5/94	0/15	0.78	-0.34
Blackcap	*Sylvia atricapilla*	0/12	0/5	0/13.5	-0.09	-1.17
Sardinian warbler	*Sylvia melanocephala*	62/75	90/87	100/95	0.08	-0.19
Bonelli’s warbler	*Phylloscopus bonelli*	0/0	0/0	47/0	-1.00	0.93
Chiffchaff	*Phylloscopus collybita*	0/1.5	0/25	0/21.5	-0.32	-1.25
Goldcrest	*Regulus regulus*	0/0	5/5	0/6.5	-0.49	-1.30
Firecrest	*Regulus ignicapillus*	0/0	8.5/17	57/48.5	-0.74	0.00
Spotted flycatcher	*Muscicapa striata*	0/0	1.5/0	1.5/0	-0.47	1.20
Long-tailed tit	*Aegithalos caudatus*	0/0	5/5	40/35	-0.81	0.14
Crested tit	*Parus cristatus*	0/0	0/0	68.5/83.5	-0.84	0.07
Coal tit	*Parus ater*	0/0	0/0	17/8.5	-0.96	0.33
Blue tit	*Parus caeruleus*	0/0	0/1.5	3/12	-0.86	-0.26
Great tit	*Parus major*	10/7	33.5/18	80/48	-0.48	0.15
Short-toed treecreeper	*Certhia brachydactyla*	0/0	0/0	60/46.5	-0.89	0.19
Golden oriole	*Oriolus oriolus*	0/0	0/0	21.5/0	-0.96	1.14
Southern grey shrike	*Lanius meridionalis*	51.5/35	28.5/19	0/0	1.24	0.06
Woodchat shrike	*Lanius senator*	10/0	0/0	0/0	1.67	1.65
Jay	*Garrulus glandarius*	0/0	6.5/3	40/43.5	-0.78	0.19
Magpie	*Pica pica*	0/0	0/0	22/10	-0.98	0.73
Chaffinch	*Fringilla coelebs*	0/14	0/12	0/38.5	-0.34	-0.87
Serin	*Serinus serinus*	18.5/8	50/19	78/10	-0.14	0.52
Greenfinch	*Carduelis chloris*	6.5/5	5/3	25/7	-0.27	0.59
Goldfinch	*Carduelis carduelis*	0/1.5	3/3.5	16.5/11.5	-0.56	0.11
Rock bunting	*Emberiza cia*	3/5	6.5/1.5	8.5/0	0.12	0.38
Ortolan bunting	*Emberiza hortulana*	7/0	5/0	0/0	1.99	1.81
Corn bunting	*Miliaria calandra*	11.5/1.5	0/0	0/0	1.87	1.16

F1, the first factor obtained from the correspondence analysis, accounted for 12.1% of total data matrix variance and represented a progressive gradient ranging from birds of open habitats (positive scores) to forest birds (negative scores). On the other hand, F2 (6.9 % of total data matrix variance) represented a gradient ranging from bird species that were widespread during the winter (negative scores) to those that were widespread during the breeding season (positive scores) (Table 1).

The seasonal changes in the open-forest species gradient (F1) differed between zones in both 1997 and 1998 (Table 2). This seasonal shift was significantly less pronounced in the unburnt zone than in F94 ($F_{1,58}$=51.20, P<0.001 in 1997; $F_{1,55}$=73.70, P<0.001 in 1998) or in F82 ($F_{1,58}$=25.81, P<0.001 in 1997; $F_{1,52}$=50.96, P<0.001 in 1998) (Fig.1). Therefore, the zones affected by fire, which had a breeding bird community clearly dominated by open and shrubby species, increased the number of forest species during the wintering season whereas the unburnt zone did not undergo any trend for this factor. Accordingly, five summer visitors were clearly associated with open spaces: Black-eared wheatear, Woodchat shrike, Ortolan bunting, Rock thrush and Tawny pipit, which whereas only two species of winter visitors were strictly linked to open spaces: Black redstart and Meadow pipit. Furthermore, many resident species that inhabited burnt zones became more scarce there in the wintering season but did not enter the unburnt zone (eventually the Dartford warbler entered), which contrasted with the observations that most winter visitors of burnt zones were typically forest species such as the Robin, Wren, Goldcrest or Blackcap.

Table 2. ANOVA models for the open-forest species gradient (F1) according to zone (unburnt zone, F94 and F82) and season (breeding and wintering). Results are given for the two periods (1997 and 1998).

Factor	d.f.	*F*	*P*
1997			
Zone	2,87	248.5	<0.001
Season	1,87	23.2	<0.001
Interaction	2,87	20.9	<0.001
1998			
Zone	2,81	175.4	<0.001
Season	1,81	50.1	<0.001
Interaction	2,81	40.6	<0.001

The seasonal changes in the gradient from birds that were frequent in the wintering season to birds that were frequent in the breeding season (F2) also differed between zones in both 1997 and 1998 (Table 3). This seasonal change was stronger in F94 than in the unburnt zone ($F_{1,58}$=11.88, P<0.01 in 1997; $F_{1,55}$=7.61, P<0.01 in 1998) (Fig. 2). However, F82 and the unburnt zone did not differ ($F_{1,58}$=0.58, P=0.810 in 1997; $F_{1,55}$=1.46, P=0.232 in 1998) (Fig. 2). Therefore, although the three study zones showed a significant change from communities characterised by summer birds in the breeding season to winter birds in the non-breeding period, this seasonal shift was significantly greater in the most recently burnt zone.

Table 3. ANOVA models for the breeding-wintering species gradient (F2) according to zone (unburnt zone, F94 and F82) and season (breeding and wintering). Results are given for the two periods (1997 and 1998).

Factor	d.f.	*F*	*P*
1997			
Zone	2,87	14.3	<0.001
Season	1,87	205.8	<0.001
Interaction	2,87	6.9	<0.01
1998			
Zone	2,81	5.8	<0.01
Season	1,81	183.8	<0.001
Interaction	2,81	3.0	0.056

The seasonal changes in richness also differed between zones in both 1997 and 1998. (Table 4). However, the change was more marked in the unburnt zone than in F82 in both years ($F_{1,58}$=6.35, P<0.05 in 1997; $F_{1,52}$=3.81, P=0.056 in 1998), and in F94 in 1998 ($F_{1,58}$=2.47, P=0.121 in 1997; $F_{1,56}$=9.34, P<0.01 in 1998) (Fig. 3). The slight trend towards an increase in richness in F94 during the 1998 wintering season (Fig. 3) was caused by an irruption of the Black redstart, a species that was not present in the winter of 1997. Therefore, although the stations situated in F82 and F94 changed their bird species composition more than those of the unburnt zone, they did not show significant seasonal changes in the total number of species.

Table 4. ANOVA models for the richness according to zone (unburnt zone, F94 and F82) and season (breeding and wintering). Results are given for the two studied periods (1997 and 1998).

Factor	d.f.	*F*	*P*
1997			
Zone	2,87	64.8	<0.001
Season	1,87	14.9	<0.001
Interaction	2,87	3.7	<0.05
1998			
Zone	2,81	55.7	<0.001
Season	1,81	2.8	<0.1
Interaction	2,81	5.8	<0.01

Finally, the seasonal changes in total bird abundance also differed between zones, although only marginally in 1998 (Table 5), when the pattern was quite different from that of the previous year (Fig.4). In 1997 the seasonal change in abundance shown by the unburnt zone was significantly different from that of F94 ($F_{1,58}$=5.16, P<0.05) and F82 ($F_{1,58}$=13.96, P<0.001). In 1998 bird abundance increased in all zones from the breeding to the wintering season. However, this increase did not differ between F82 and the unburnt zone ($F_{1,52}$=0.04, P=0.945), whereas it did between F94 and F82 ($F_{1,55}$=5.92, P<0.05) and between F94 and the unburnt zone ($F_{1,55}$=3.70, P=0.059). Thus, the most remarkable pattern observed was the high interanual variation in bird abundance in the two burnt zones.

Table 5. ANOVA models for the abundance according to zone (unburnt zone, F94 and F82) and season (breeding and wintering). Results are given for the two periods (1997 and 1998).

Factor	d.f.	*F*	*P*
1997			
Zone	2,87	57.5	<0.001
Season	1,87	0.1	n.s.
Interaction	2,87	9.6	<0.001
1998			
Zone	2,81	17.3	<0.001
Season	1,81	69.3	<0.001
Interaction	2,81	2.9	0.58

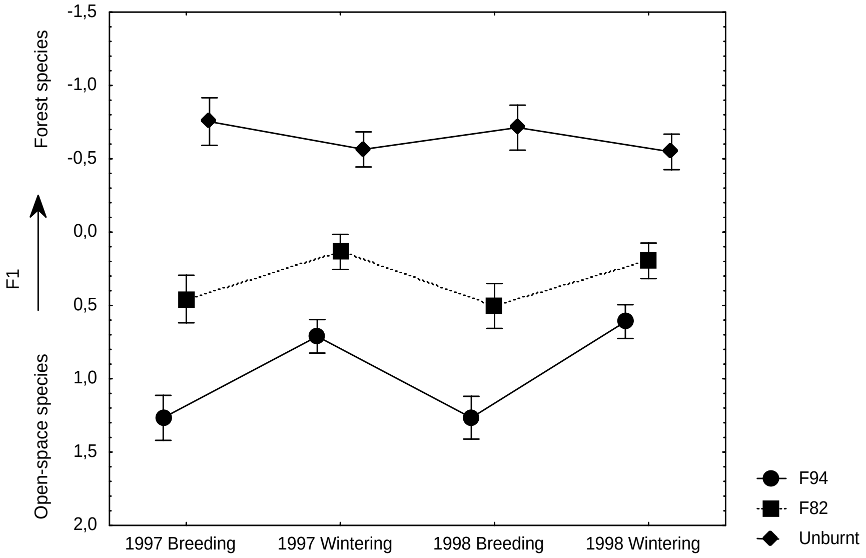

Figure 1. Changes in the gradient from birds of open habitats (positive scores) to forest birds (negative scores) (F1) in the three study zones. Bars indicate standard error.

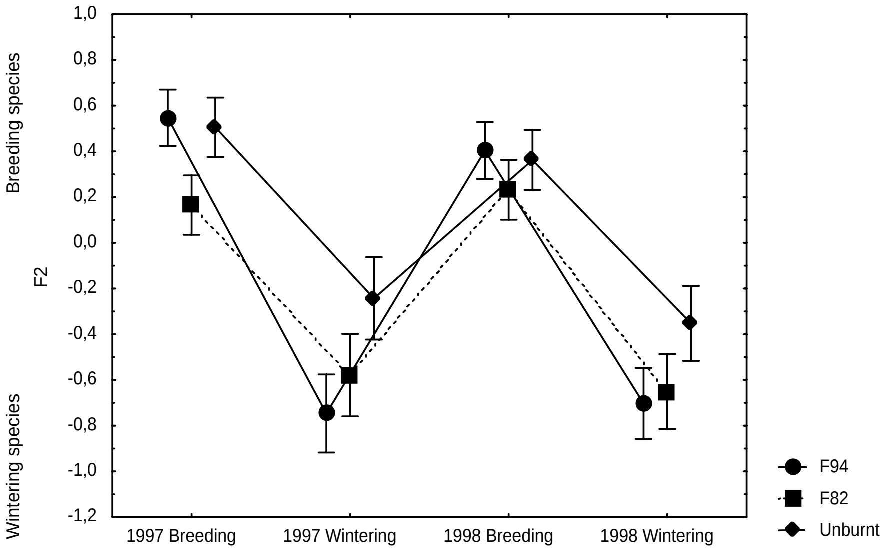

Figure 2. Changes in the gradient from birds that were widespread during the winter (negative scores) to birds that were widespread in the breeding season (positive scores) (F2) in the three study zones. Bars indicate standard error.

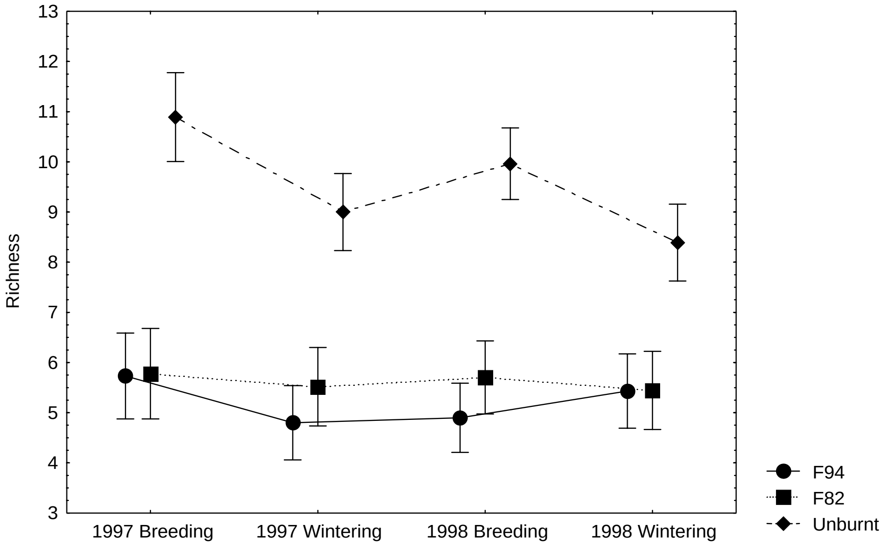

Figure 3. Changes in richness in the three study zones. Bars indicate standard error.

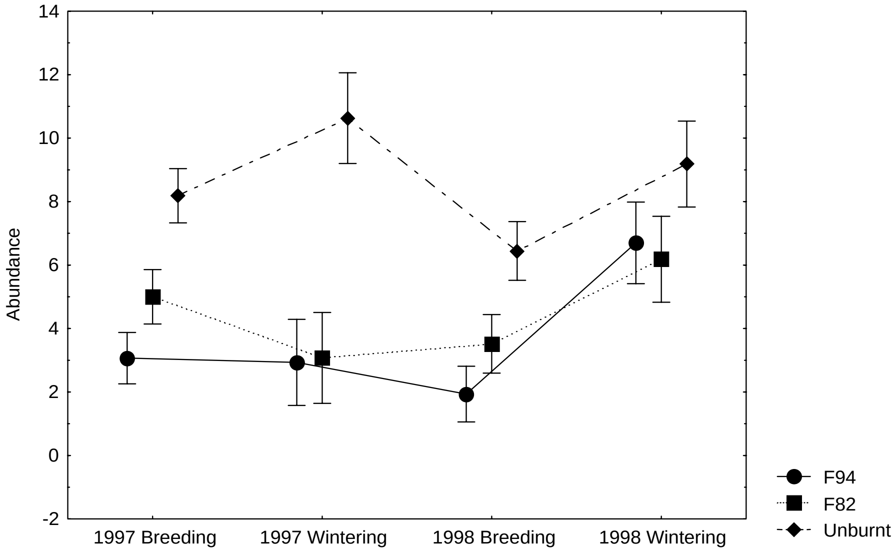

Figure 4. Changes in bird abundance in the three study zones. Bars indicate standard error.

DISCUSSION

Our results indicate that burnt zones show a noticeable shift towards a more “forested” species composition from the breeding to the wintering season, whereas the unburnt zone did not show any significant trend. Therefore fire increased the “open-species” component of bird communities but to a greater extent during the breeding season. Our data show that burnt zones are comparatively rich in forest species in the wintering season. These species seemed to enlarge niche breadth and were also found in unforested habitats during this period. The finding that the range of habitats occupied by species is less restricted in the wintering than in the breeding season is not new (Alatalo 1981, Rice *et al*. 1983, Bilke 1984), but interestingly, our results show that this niche shift is not the same for all ecological categories and, at least in our case, was more common from forest to open habitats than vice versa.

We show that all study zones undergo a seasonal change from communities characterised by summer visitors in the breeding season to those characterised by winter visitors in the wintering season. Nevertheless, this shift was more pronounced in F94, which indicates that the seasonal turnover of bird communities is higher in recently burnt zones. Migration itself is essentially an strategy to adapt to fluctuations in food supply that, at least some years, might lead to the extinction of local populations (Stocker & Weihs 1998). The Mediterranean region, which is an important scene of Palearctic migration, is an essential wintering ground for many bird species (Lövei 1989, Blondel & Aronson 1999). Nevertheless, although non-resident birds became extraordinarily abundant in many Mediterranean habitats, there are marked differences in non-resident bird abundance in relation to habitat (Lövei 1989). For example, Herrera (1978) found in Iberian holm-oak forests that the ratio between resident and non-resident birds was balanced in favour of the former. He proposed that this may be the result of a low degree of seasonality and high predictability of food supply. According to this author, non-resident species are more generalist, exploiting diverse and spatially unpredictable resources. Mönkkönen & Helle (1989) showed that the higher predictability of resources in forests was not sufficient to explain residency patterns, since North-American forest bird communities were dominated by migrant species, whereas European ones were dominated by resident species. These authors pointed out the role of landscape in the wintering grounds since the proportion of forests is much lower in Africa than in Central and South-America. Therefore, resource predictability in the Mediterranean forests of Western Palearctic and the scarcity of this type of habitat in African wintering grounds may be under the high sedentarity of the bird communities inhabiting unburnt areas compared with recently burnt ones.

The seasonal shift in richness was clear and repeated in the two census years in the unburnt zone, where the number of species decreased from the breeding to the wintering season. In contrast, the burnt zones, where species composition varied more between seasons, showed an almost constant richness throughout the study period. Our results differ from those reported by Prodon *et al*. (1987) in cork-oak forests, in which maximum bird richness was found in the breeding season in both burnt and unburnt zones. However, as Prodon et al. revealed in the same work and in contrast to calcareous shrublands, post-fire avian dynamics is accelerated fast in cork-oak forests due to the capacity of this tree to sprout from main branches after fire.

Seasonal patterns in relation to F1, F2 and richness, that is, in relation to bird assemblages were very repeatable during the two study periods. This contrasts with a lower overall annual cyclicity in bird abundance. This is an interesting observation, since it reveals two distinct processes in the structuring of bird communities. On the one hand, bird species composition, which has been described as being shaped by the physical structure of habitat (McArthur & McArthur 1961, Wilson 1974, Wiens 1989). On the other hand bird abundance, which is thought to be related to either habitat productivity (Nilsson 1979) or, far from the level of carrying capacity, shaped via stochastic processes (Wiens 1974, Jarvinen 1978). There is an underlying but interesting difference between the patterns that influence both bird species composition and bird abundance: in the absence of disturbances such as fire, physical structure is supposed to remain quite stable during consecutive years whereas stochastic processes are, by definition, quite unpredictable and may appear in short periods. For example, the amount of some fleshy-fruit crops, which are a basic food resource for many Mediterranean birds during the wintering season (Blondel & Aronson 1999), vary considerably and are only abundant some years (Herrera 1994). Therefore, some seasonal variation in bird abundance of habitats involved in post-fire dynamics may be hidden by differences in food supply or by stochastic processes which influence bird populations directly or indirectly through resources. The increase in bird abundance observed in the two burnt zones should, therefore be considered within this context, more than as a result of succession itself. However, it is remarkable that the pattern of abundance in the unburnt zone was quite repeatable during the two study periods, which suggests a higher annual cyclicity in resource availability in unburnt areas. Again, this result suggests that these unburnt areas of the Mediterranean are more stable and undergo fewer productivity oscillations than those affected by fire. Indeed, it is also interesting to note that in 1998, F94 showed a higher increase in bird abundance than F82, which suggests that recently burnt areas may be subjected to greater annual oscillations than those burnt longer ago.

In contrast to our results, García (1997) found that in both, burnt and unburnt zones of holm-oak forests of the Iberian plateaux, bird abundance peaked during the breeding season. This pattern might be related to the distinct climate, since the Garraf Natural Park is much warmer in winter than the Iberian plateaux. Nevertheless, in areas with a similar mild climate in southern France, Prodon *et al.* (1987) and Pons & Prodon (1996) also reported that in both burnt and unburnt areas maximum bird abundance was observed in spring and minimum in winter. These trends, in contrast to the pattern observed in our unburnt zone for 1997 and 1998 and that found in burnt zones in the 1998, may not only be associated with climate. According to the plant species composition cited in their articles, fleshy-fruit producing plants are much less abundant in these acid-soil areas of southern France than in our calcareous Iberian study area. Therefore, we suggest that, besides climate, plant species composition, which is also highly influenced by lithology, may play a key role in the seasonal patterns of bird abundance.

In conclusion, our results are consistent with the classical view of succession that states that undisturbed systems internalise better environmental fluctuations without changing their structure than recently disturbed ones (Margalef 1968, Odum 1969) since seasonal variations in bird communities were more marked in burnt than in unburnt zones.

Acknowledgements

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Fluctuating asymmetry in Sardinian Warblers *Sylvia melanocephala* inhabiting two shrublands affected by fire[1]

Abstract

The effects of post-fire changes in vegetation and habitat quality on the developmental stability of individual birds have not been assessed to date. Here we compare fluctuating asymmetry in tail feathers of Sardinian Warblers *Sylvia melanocephala* inhabiting two shrubby zones, the first burned in both 1982 and 1994 and the second only in 1982. Juveniles with unmoulted rectrices showed significantly higher levels of tail feather asymmetry in the zone burned in 1994. This result is consistent with the hypothesis that recently burned shrublands offer lower quality habitats for this species. Because feather asymmetry was positively and significantly related to the abundance of low shrubs up to 50 cm tall, we suggest that juvenile assessment of habitat quality is primarily based on the structure of the shrub layer.

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[1] With Lluís Brotons. University of Barcelona. Bird Study 2001 (in press).

INTRODUCTION

Fire is a natural phenomenon that has greatly influenced the development of Mediterranean ecosystems. The study of the effects of fire on Mediterranean bird communities has mainly focused on species turnover, variations in specific abundance throughout succession and the association between changes in vegetation structure and community composition (Lawrence 1966, Stanton 1986, Prodon et al. 1987, Vicente 1991, Pons & Prodon 1996, Izhaki & Adar 1997). After fire, the bird community changes progressively from grassland species to shrubby and forest species. However, while some species appear quite soon after fire and are able to persist as vegetation develops, other species disappear (Prodon et al. 1987). Perhaps one of the Mediterranean species that best exemplifies the first pattern is the Sardinian Warbler *Sylvia melanocephala.* Several studies have shown that this generalist species reaches maximum densities in habitats containing a high proportion of large or medium height shrubs (Cody & Walter 1976, Prodon & Lebreton 1983, Martin & Thibault 1996). Abundance estimates have commonly been used as a measure of habitat quality at each successional stage following post-fire dynamics (Prodon et al. 1987, Vicente 1991, Pons & Prodon 1996), but such estimates do not provide direct information about the quality of individuals in distinct habitats (Van Horne 1983, Wiens 1989). Therefore, individual measures, such as developmental stability are believed to provide a better estimate of the magnitude of habitat quality than estimates of population size (Clarke 1992). Fluctuating asymmetry, the most commonly used estimate of developmental stability, is defined as random deviations from perfect symmetry in a bilateral trait (Palmer & Strobeck 1986). Fluctuating asymmetry on the growth of right and left side traits is sensitive to a large number of environmental factors (e.g. adverse temperature, nutritional deprivation, habitat disturbance or high population density) and therefore could be used as a technique for monitoring habitat quality (Leary & Allendorf 1989, Clarke 1993, Polak & Trivers 1994, Clarke 1995, Freeman et al. 1995, Møller & Swaddle 1997, Carbonell & Telleria 1998, Carrascal et al 1998, Lens et al. 1999). Traits that are maintained throughout life, such as skeletal characters, exhibit extremely stable development trajectories and hence very small levels of fluctuating asymmetry. In contrast, temporary traits like feathers are less stable and usually exhibit larger asymmetries (Clarke 1995). We collected tail feathers instead of wing feathers because asymmetry levels are much greater in the former (Møller a& Höglund 1991). Tail feather asymmetry has been reported to reduce avian performance under controlled experimental conditions (Møller 1991, Evans et al. 1994) and to increase mortality under situations of intense natural selection (Brown & Brown 1998). Outer tail feathers were chosen because asymmetry in central feathers is far less costly for an individual than the same absolute asymmetry in outer feathers (Møller & Swaddle 1997).

To our knowledge, the effects of post-fire changes in vegetation and habitat quality on the developmental stability of individual birds have not been assessed to date. Here we aim to compare the feather asymmetry of Sardinian Warblers inhabiting two shrublands, the first burned in both 1982 and 1994 and the second only in 1982. Specifically we test the hypothesis that, as suggested by earlier density estimates, the zone most recently affected by fire is less appropriate for this species and results in increased levels of feather asymmetry.

METHODS

Species

The Sardinian warbler is a generalist species that is widely distributed throughout the Mediterranean Basin and is able to live in habitats as distinct as dense forests, low shrubs, towns or even desert fringes (Cramp 1992). In spite of such a variety of possible habitats, the Sardinian Warbler is usually unable to breed in the first year after a severe fire (Prodon et al. 1987, Prodon & Lebreton 1983, López & Guitian 1988, Sgardelis & Margalis 1992) However, Pons and Prodon (1996) found this species persisting after fire in small remnants of unburned vegetation.

Study sites

Field work was carried out from August 1999 to January 2000 in the Natural Park of Garraf, situated 20 km to the south of the city of Barcelona (NE Iberian Peninsula). This natural park (41º 15' N, 1º 55' E) has been affected by two extensive fires in recent decades: the first burned 10,000 ha in 1982 and the second, which was located entirely over the area affected by fire in 1982, burned 5,000 ha in 1994. Although both areas were burned in 1982, to simplify the terminology, from here onwards these two zones are called burned (the one burned in 1994) and unburned (the one unburned in 1994). The similarity in relief and in plant species composition (unpublished data) and the proximity of both areas suggested that, at least for birds, the main difference between these two areas was associated with the changes in vegetation structure caused by the 1994 fire.

In a study carried out during the breeding season of 1998, we estimated Sardinian Warbler abundance in 120 point-counts with several counting bands (Bibby et al. 1992). We estimated 1.5 individuals/10ha in the burned zone and 12.5 individuals/10ha in the unburned zone. This data suggested that the burned zone was a habitat of lower overall quality for this species. Therefore, this natural park provided an appropriate opportunity to study variations in the asymmetry of the Sardinian Warblers inhabiting zones which have been affected by fire.

Bird measurements

We selected the trapping sites randomly within each of the two areas (the burned and the unburned). Birds were captured using mist-nets and aided using song play-back and were then banded for individual recognition with aluminium rings. Following Svensson (1992), birds were aged and weighed, and tarsus, wing and tail lengths were measured. Measurements were always taken by the same person.

The length of tail feather was accurately measured twice (a second measurement was done following completion of the first measure of all feathers) with a slide calliper. The repeatability of feather length was assessed following the methodology described by Lessells and Boag (1987). However, low measurement error in component traits (i.e. length of right and left sides) does not ensure low measurement error in the derived trait (i.e. asymmetry), specially if this trait is so small (Swaddle et al. 1994). Therefore we assessed asymmetry repeatability by means of the mixed-model ANOVA proposed by Swaddle et al (1994). We tested the normality of feather asymmetry (difference in length of left and right feathers) by normal probability plot and the Shapiro-Wilks's test. We also tested the non-directionality of the asymmetry obtained by means of the t-test for deviation from the null hypothesis of average asymmetry equal to zero. An asymmetry index was assessed as the absolute difference in length between left and right tail feathers. This asymmetry index was not corrected for size effects because no significant relationship between asymmetry and size was found.

We considered the asymmetry of three groups of individuals separately: adults, first year birds with moulted tail feathers (moulted juveniles) and first year birds with unmoulted tail feathers (unmoulted juveniles). We selected these three classes because the growth of their tail feathers may be subjected to distinct stress conditions. On the one hand, unmoulted juveniles retain rectrices grown during the nestling period, when competition from sibs and the pressure to leave the nest as rapidly as possible (because of predation risk and future settlement) represent an important source of stress which influences feather growth. On the other hand, the moult of adults and moulted juveniles may be under distinct stress conditions because they may differ in their capacity to overcome environmental constraints and in their competitive ability (Breitwisch 1989).

Vegetation sampling

The vegetation structure at each bird trapping station was measured within a 25 m radius around the observer. We estimated the cover of different vegetation layers (0-0.25 m, 0.25-0.5 m, 0.50-1 m, 1-2 m, 2-4 m, 4-8 m, 8-16 m) and rock layer as habitat variables. Within each layer, the relative cover value was defined as the projection of the foliage volume of the layer (or rock layer) onto a horizontal plane. We estimated this projection by comparing with the reference chart following Prodon and Lebreton's procedure (1981). According to these authors, this method allows the observer to attain a reliability of ±10 %.

Data analysis

Biometric measurements and fluctuating asymmetry indexes were compared between the birds captured in the burned and unburned zones by means of the Student's t-test for independent samples. We decided to perform a test for each group, because low sample sizes in two of the groups might have very misleading the interactions calculated through a two-way ANOVA. To assess the role of sample size on the lack of significance obtained, we also calculated the statistical power of the test given the data available in order to find the probability of rejecting the null hypothesis when it was true (Cohen 1988).

We performed a principal component analysis (PCA) for vegetation structure, thus minimising intercorrelation of vegetation variables as well as determining the important features of structure, while reducing the number of variables. The initial factors of each PCA were rotated by the varimax procedure because rotated factor loadings were conceptually simpler than unrotated ones. In order to identify relationships between the outer tail feather asymmetry of Sardinian Warblers and the features of the site they were captured, we used a generalised linear model (McCullagh & Nelder 1983). The asymmetry index was used as dependent variable and a best subsets procedure was carried out to select only significant variables from the initial set of predictors that included the two main factors of the PCA performed previously. Statistical analyses were run with Statistica Statsoft, Inc 1999.

RESULTS

A total of 57 Sardinian Warblers were captured: 12 adults, 29 unmoulted juveniles, 14 juveniles with moulted outer tail feathers, one juvenile with only one moulted outer tail feather and another which was not included in the analysis because we were unable to ascertain if it was an adult or moulted juvenile. There were no significant differences in body weight, tarsus, wing or tail length between the individuals captured in the burned zone (n=33) and those captured in the unburned zone (n=24) (Table 1).

The number of individuals used in asymmetry analyses were reduced to 51 because 6 birds showed damaged tail feathers and their lengths could not have been correctly measured. The repeatability of tail feather length was very high (r=0.99 on left rectrices and r=0.99 on right rectrices). Using the model proposed by Swaddle et al. (1994), estimated asymmetry of these feathers was also very repeatable and significantly higher than expected from the estimated measurement error ($F_{50,100}$=138, P<0.0001). The asymmetry of rectrices (difference in length of left and right feathers) reached a normal distribution as shown by normal probability plot and the Shapiro-Wilks's test (W=0.975, P=0.377) and was not directional because it was centred around zero (t-test against the null hypothesis of average asymmetry equal to zero: t_{98}=-0.555, P=0.583). Without considering habitat type, overall asymmetry estimates did not differ significantly between moulted juveniles, adults or unmoulted juveniles ($F_{2,45}$=1.21, P=0.306). However, this pattern changed depending on the habitat in which they were captured. The outer tail feathers of unmoulted juveniles were more asymmetric in those captured in the burned zone than in those in the unburned zone (t_{24}=-2.29, P=0.030) although neither adults (t_8=0.88, P=0.406) nor juveniles with moulted tail feathers (t_{11}=-0.80, P=0.438) showed differences in asymmetry in either habitat (Fig. 1). Due to the low sample sizes of adults and moulted juveniles the power of our analyses was also quite low. Therefore, for a given α=0.05, the probability of finding a significant difference when the difference did exist was β=0.39 for adults and β=0.33 for moulted juveniles.

Table 1. Morphological measurements of Sardinian Warbler captured in burned (n=33) and in unburned (n=24) zones. Values: mean (sd).

	Burned	Unburned	t-test	P
Body mass (g)	12.56 (0.80)	12.55 (0.64)	0.01	0.991
Tarsus length (mm)	20.01 (0.90)	19.95 (0.63)	0.31	0.756
Wing length (mm)	57.90 (1.35)	58.69 (1.15)	-1.92	0.059
Tail length (mm)	62.30 (1.85)	63.15 (2.00)	-1.20	0.235

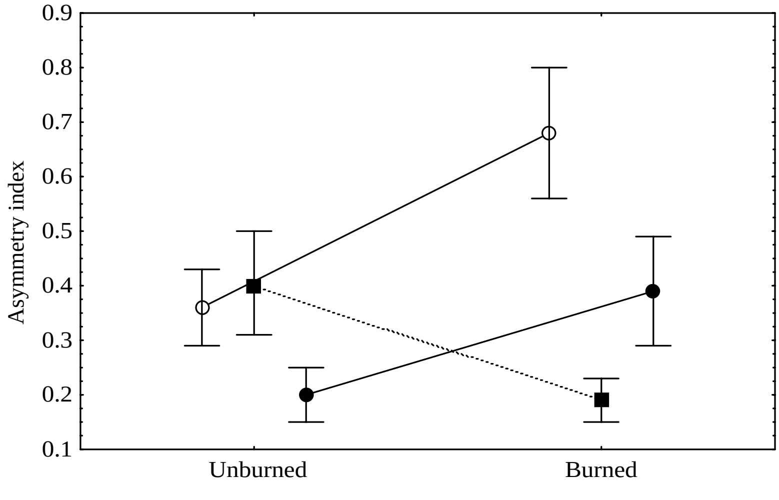

Figure 1. Effects of age/moult and habitat on tail feather asymmetry. Open circles correspond to unmoulted juveniles, solid circles to juveniles with moulted outer tail feathers and solid squares to adults. Values are means (±se).

Feather asymmetry and vegetation structure

The first factor (SF1) obtained from the PCA of structural data, which accounted for 48.18% of total data matrix variance, was interpreted as a gradient from low shrubs (less than 50 cm tall) to large shrubs and small trees (Table 2). The second factor (SF2), which accounted for 17.03% of total data matrix variance, represented a gradient from bare soils covered by rocks or small plants up to 50 cm tall to medium and large shrubs up to 2 m tall (Table 2). The main difference between these two factors was that SF1 incorporated large shrubs and trees as negative values, while SF2 took lower layers (rocks, grasses and small ligneous plants up to 25 cm) as positive values.

Table 2. Correlations between the relative cover of each structural layer (vegetation layers and rock layer) and the first two factors of the correspondence analysis (SF1 and SF2).

	SF1	SF2
Rock	0.197	0.590***
0.00-0.25	0.014	0.845***
0.25-0.50	0.697***	0.387**
0.50-1.00	-0.360**	-0.772***
1.00-2.00	-0.799***	-0.447**
2.00-4.00	-0.952***	0.049
4.00-8.00	-0.662***	-0.185
% Variation explained	49.87	17.04

*P<0.05; **P<0.01; ***P<0.001

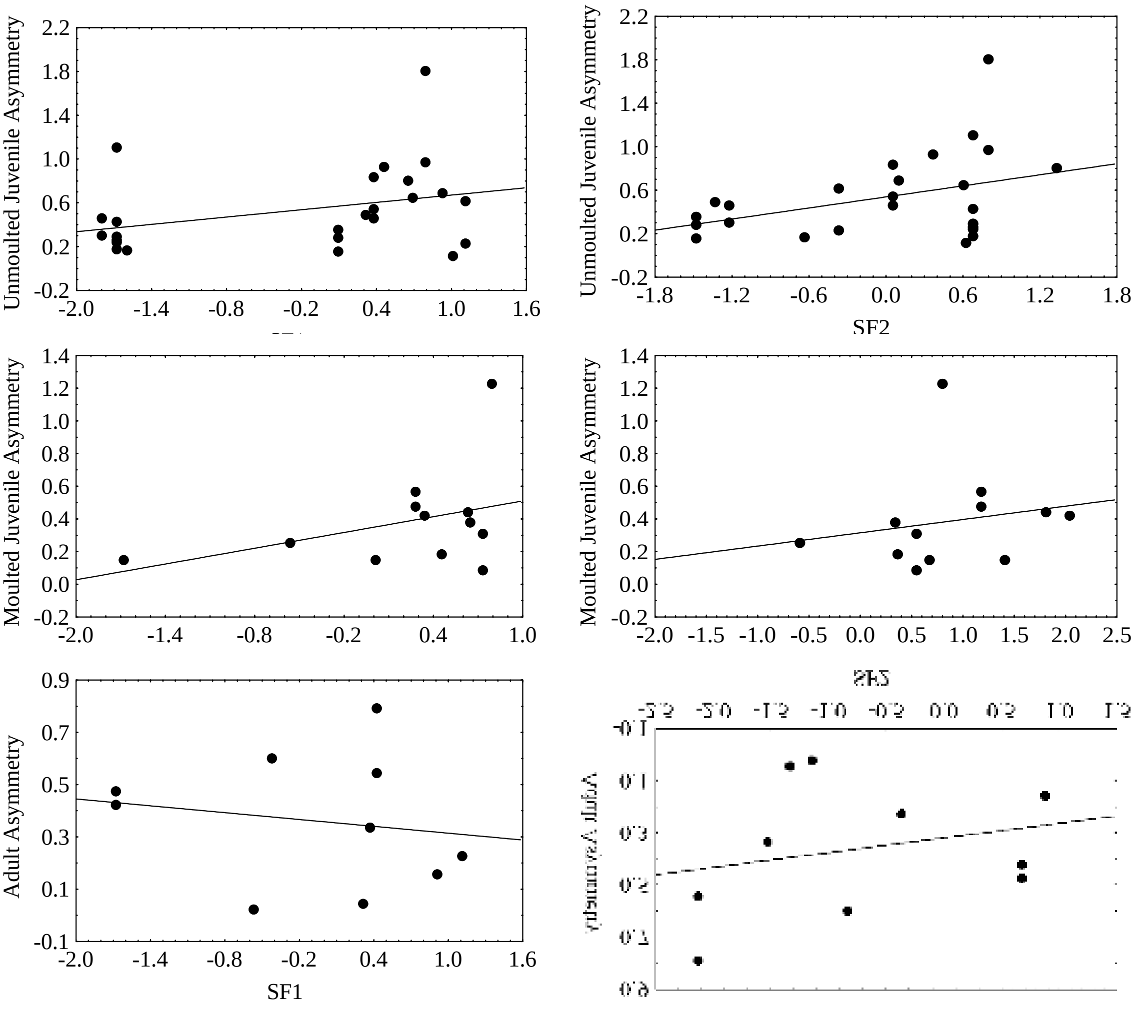

Figure 2. Asymmetry-habitat structure plots. Significant associations were only found for SF1 and SF2 in unmoulted juveniles (see results).

The initial set of predictors of the generalised linear model applied to the asymmetry index included the two structural factors (SF1 and SF2). Both in adults and moulted juveniles, the analysis of feather asymmetry in relation to these predictors failed to show any significant association, and both were omitted from the initial model. However, in the analysis performed with unmoulted juveniles, vegetation structure was found to be significantly associated with feather asymmetry (SF1, Chi square=4.37, P=0.036, estimate of 0.221; SF2, Chi square=5.65, P=0.017, estimate of 0.383) (Fig. 2). Therefore tail feather asymmetry in unmoulted juveniles was significantly and positively associated with SF2 and SF1. This result showed a clear association between the asymmetry of unmoulted juveniles and the cover of low vegetation layers, that is to say, unmoulted juveniles had more asymmetric tail feathers in sites where shrubs were mainly up to 50 cm tall.

DISCUSSION

Our results showed a significant association between tail feather asymmetry of Sardinian Warbler juveniles with unmoulted rectrices and vegetation structure following post-fire dynamics. On the one hand, more asymmetric unmoulted juveniles were captured in the burned zone, where the shrub layer was poorly developed, with only some medium size shrubs (1-2 m tall) emerging from continuous low vegetation of up to 50 cm of height. On the other hand, less asymmetric unmoulted juveniles were captured in the unburned zone, where shrubs formed a uniform layer between 1 and 2 m, with some scattered taller young trees.

The analyses performed with adults and moulted juveniles showed no conclusive differences in feather asymmetry between areas. Since asymmetry estimates were not much lower than those of unmoulted juveniles, we believe that this result mainly arises as a consequence of the low power of the tests. Further studies are needed to shed more light on this aspect.

Several studies have shown the usefulness of individual asymmetry estimates in detecting habitat quality. For example, Carbonell and Telleria (1998, 1999) found that the values of fluctuating asymmetry for mass/length ratio and for tarsus length in Blackcaps *Sylvia atricapilla* were largest in the drier regions of Spain, suggesting that this species was under greater stress when close to its southern range boundary. Lens et al. (1999) found that the asymmetry in the individuals of seven bird species passively captured using mist-nets was related to the levels of degradation and fragmentation of the afrotropical forests where they were trapped. The observation that unmoulted Sardinian Warbler juveniles were more asymmetric in the recently burned zone is consistent with the hypothesis that recently burned areas are in general of lower quality for the species and that the species is less abundant there than in later stages following post-fire vegetation development. Furthermore, the association found between feather asymmetry and vegetation structure strongly suggests that the differences detected between areas in relation to post fire dynamics are due to the link between habitat quality and shrub development in Sardinian Warbler juvenile settlement.

Although the Sardinian Warbler is a generalist species and is able to adapt to a wider range of habitats than any other Mediterranean *Sylvia* species, its optimum habitat is usually characterized by greater vegetation heights than those selected by the Dartford Warbler *Sylvia undata* (Cody & Walter 1976, Walter 1988, Martin & Thibault 1996). In a study conducted during the 1998 breeding season, we estimated that the ratio Dartford Warbler abundance / Sardinian Warbler abundance was four times higher in the burned than in the unburned zone. Furthermore, Dartford Warbler abundance was positively and significantly correlated with the presence of low shrubs between 25 and 50 cm tall whereas Sardinian Warbler abundance was positive and significantly correlated with the presence of medium and large shrubs. Therefore, in low shrubby habitats, competition with Dartford Warbler is likely to be strong because this species is abundant and no taller shrubs are available for the Sardinian Warbler. According to Cody and Walter (1976), the presence of the Dartford Warbler may influence Sardinian Warbler niche breadth. Indeed, Sardinian Warblers coexisting with Dartford Warblers in low shrubby habitats foraged on the few larger shrubs that protruded from the low vegetation canopy and had larger territories than those from more uniform medium shrubby areas (Cody & Walter 1976, Martin & Thibault 1996). Flying from one protruding shrub to another in a large territory may involve higher predation risk than the use of continuous shrubby territories. Therefore, we suggest that the association between the quality of unmoulted juveniles and vegetation structure may be closely related to the relative disadvantages (competition and predation) of this type of habitat.

Two non-mutually exclusive hypotheses could explain the origin of the differences in asymmetry estimates of juvenile Sardinian Warblers in the two areas studied. (1) Juveniles of lower quality coming from other habitats may settle in recently burned areas, or (2) Offspring born in recently burned areas are of lower quality and later settle in such areas. In reference to these two hypotheses Møller and Swaddle (1997) reported evidence that enhanced levels of asymmetry decrease fitness and thus influence bird competitive ability for settling in a habitat. Møller (1995) studied the asymmetry of European blackbirds *Turdus merula* in a mosaic of habitat fragments. In his study, nestlings born in small habitat fragments were more asymmetric than nestlings from large ones, and recruitment was also different with respect to morphological asymmetry, small habitat fragments being mainly occupied by individuals of inferior competitive ability.

The settlement of juvenile Sardinian Warblers may be influenced by physical condition and individuals with poor competitive ability which are forced to settle in poorer quality habitats than those with better body conditions. We have not obtained data to distinguish between the two hypotheses exposed as the origin of the lower quality of unmoulted juveniles in more recently burned area. Nevertheless, in a study conducted in 1998/99 we found that Sardinian Warbler abundance did not change significantly from the breeding season to the non-breeding season in the unburned area, whereas its abundance was much greater in the non-breeding (14.0 ind/10 ha) compared to the breeding season (1.5 ind/10 ha) in the burned area. Gargallo (pers.comm.) found a similar pattern in the Balearic Islands where, after the breeding season, Sardinian Warbler juveniles were much more abundant in low quality habitats, which may act as a sink for juveniles due to stronger competition with adults in better habitats. Low adult densities in lower quality habitats allowed juveniles to use seasonal available resources like fleshy fruits. Therefore, these data suggest that some of the juveniles of lower quality found in the burned zone actually originated in better habitats such as unburned areas. However, with the evidence collected so far, it is possible that juveniles are born in the same areas where they settle in autumn.

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Effects of fragmentation on forest bird diversity in Mediterranean areas affected by wild fires[1]

Abstract

Fire is a key mechanism creating and maintaining habitat heterogeneity in Mediterranean landscapes by turning continuous woody landscapes into mosaics of forests and shrublands. Due to the long historical role of fires in the Mediterranean, we hypothesised a moderate negative effect of this type of perturbation on forest bird distribution at a landscape level. We conducted bird censuses in Aleppo pine forest patches surrounded by burnt shrublands and studied the relationships between three ecological groups of bird species (forest canopy species, forest understorey species, and ubiquitous species) and the features of local habitat, patch and surrounding landscape. Regarding local habitat components, canopy species were positively associated with tall pines while understorey species with the cover of shrubs and plants from Holm-oak forests. Forest birds were positively related to patch size and irregular forest shapes, that is to say, with high perimeter/size ratios. Thus, these species did not seem to perceive edges as low quality but rather favourable microhabitats. We did not detect any negative effect of isolation or cover of woodlands in the landscape on the presence of forest species. Finally, only local habitat factors entered the model for ubiquitous species. We suggest that mosaic-like landscapes shaped by fires in the Mediterranean basin are not associated with negative effects of fire-induced fragmentation on forest birds other than those related with habitat loss.

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[1] With Lluís Brotons. University of Barcelona. Submitted

INTRODUCTION

Habitat fragmentation consists of the subdivision of a continuous habitat into smaller pieces, thereby altering the landscape structure through a loss of a given habitat and changes in the spatial configuration of remnant patches (Saunders 1991, Andrén 1994). Several studies have found that forest fragmentation has deleterious consequences for forest birds, but these have been basically carried out in landscapes directly modified by human activities such as farming (e.g. Bellamy et al. 1996, Díaz et al. 1998, Tellería and Santos 1999), timber exploitation (e.g. Askins et al. 1987, Jokimäki and Huhta 1996, Schmiegelow 1997) or urbanisation (e.g. Friesen et al. 1995, Mancke and Gavin 2000), and data for landscapes where forests have been fragmented by natural disturbances such as fires are scarce. The historical background of the first three types of fragmentation differed notably from that associated with fire-shaped landscapes, possibly inducing different responses of vertebrates to landscape structure (Mönkkönen & Reunanen 1999). Man-induced fragmentation associated with processes such as farming or logging are historically recent (but see Mönkkönen and Welsh 1994) whereas fire is a natural disturbance involved in the dynamics of many ecosystems (Kozlowski and Ahlgren 1974).

Wildfires turn continuous blocks of forest into fragmented ones and configure land mosaics which are characterised by remnant forest patches within a burnt shrubby matrix (Forman 1995). Fire has lost part of its historical role in many developed countries as a result of present landscape management and fire-control policies (Hunter 1993). In contrast, current land abandonment in Euro-Mediterranean countries have led to the encroachment of formerly cultivated lands by woody vegetation (Preiss et al. 1997) which, together with a general climate trend towards drier and warmer conditions (Piñol et al 1998), has greatly contributed to increasing the extent of burnt areas in recent decades. However, fire-induced forest fragmentation cannot be considered recent process but rather a phenomenon which is intrinsically linked with the dynamics of Mediterranean ecosystems that humans have enhanced during their long-lasting activity in the Mediterranean Basin (Trabaud 1981, Blondel and Aronson 1999). The study of the effects of fires on Mediterranean bird communities have focused on the successional dynamics of burnt areas itself (e.g. Lawrence 1966, Prodon et al 1987, Pons and Prodon 1996, Izhaki and Adar 1997). Nevertheless, no attempt has been made to study the consequences of the fire regime at a landscape level on the bird assemblages inhabiting forests fragments within a burnt matrix.

If the fragmentation provoked by natural disturbances such as fire has been incorporated into the habitat selection processes of forest bird species, we expect that, apart from habitat loss, this type of fragmentation will cause hardly any negative impacts on Mediterranean forest birds. Specifically, we address the following questions: What are the independent effects of local habitat, patch and landscape structure on bird assemblages in landscape mosaics generated by fire? Are bird communities negatively affected by habitat loss and the concomitant increase in edges? Is the shrubby matrix permeable enough to reduce the effects of patch isolation on forest birds? Given that burnt habitats are dominated by shrubs, we also predict that forest species foraging in the shrubby understorey will be less affected by forest fragmentation than forest canopy species.

METHODS

Study area

Fieldwork was carried out in the coastal mountains located between Barcelona and Tortosa cities, in the Northeast of the Iberian Peninsula (41º N, 1º E) (Fig. 1). The study area ranges from 100 to 700 m a.s.l and is located between the mesic "meso-Mediterranean" and the xeric "thermo-Mediterranean" life zone. The first is characterised by closed canopy Holm-oak (*Quercus ilex*) forests, whereas the second, is dominated by dense, low height, coastal shrublands of Wild Olive Tree (*Olea europaea*), Lentisk (*Pistacia lentiscus*) and Mediterranean Dwarf Palm (*Chamaerops humilis*) among others (Blondel and Aronson 1999). These two types of vegetation were formerly dominant in the landscape but, like many other areas of the Mediterranean Basin, the original landscape was changed by human activity several millennia ago and since then it has undergone continuous redesign. The mountains of the study areas were heavily cultivated until the beginning of twentieth century. From then on, it has started a progressive depopulation of most rural areas that has allowed the recovery of secondary natural vegetation. Today, secondary low shrubby formations (*Rosmarino-Ericion*) and Aleppo pine (*Pinus halepensis*) forests have dominated the landscape. These formations are prone to affection by wild fires, which burn large areas in the Mediterranean basin periodically. In forest areas dominated by Aleppo pines, wild fires kill the trees and burnt completely the aerial parts of shrub. However, because most of shrub species sprout from unaffected roots, fires fragment forests by creating a burnt, very dense and low matrix (Trabaud 1981). In case of recurrent fires, Aleppo pine, which is not a sprouting species, is not able to grow enough to reproduce and shrubby areas evolve towards a more permanent shrubland without a tree layer. The study area was characterised by the presence of remnant Aleppo pine forests, which were aggregated or isolated to a variable degree, and surrounded essentially by a burnt shrubby matrix.

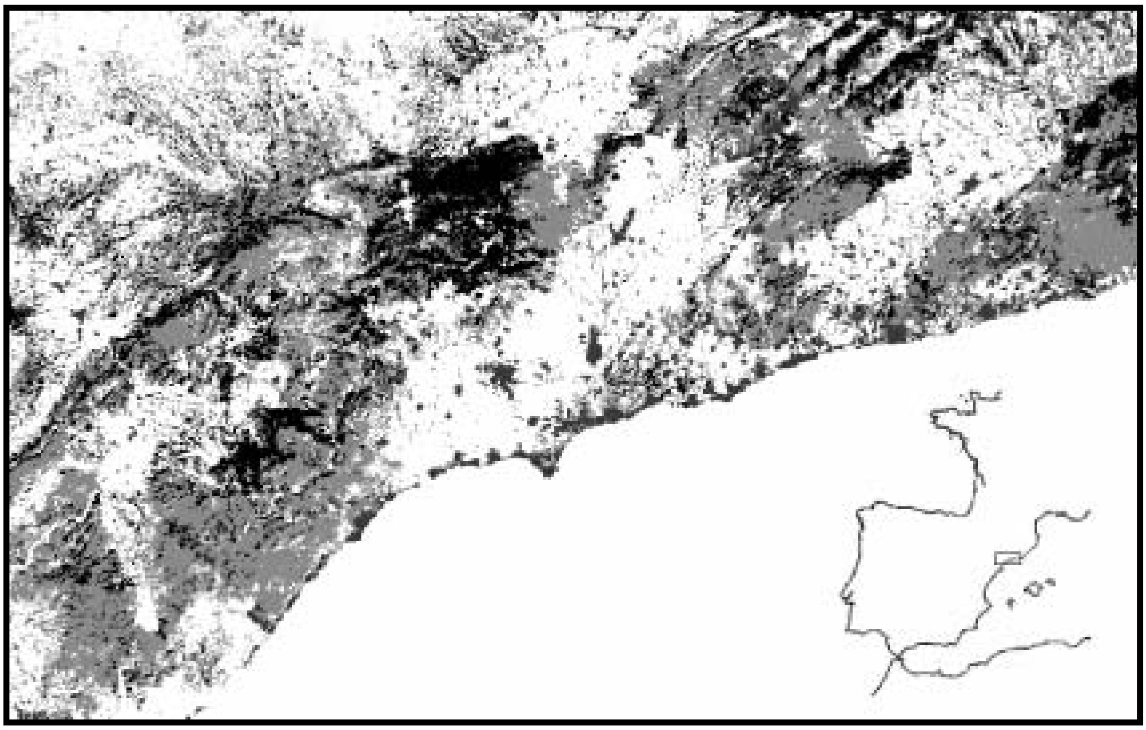

Fig. 1. Geographic location and vegetation map of the study area, based on reclassification of Landsat categories. Black zones represent forests, soft grey represents shrublands burnt in recent decades, dark grey represents urbanised areas and white zones represent farmland. A high component of forest fragmentation due to fires can be easily appreciated in this image.

Study design

By means of aerial photographs (1:25 000, Institut Cartografic de Catalunya, 1993 and 1997) we searched for forests patches surrounded by a burnt shrubby matrix. For the present study, we selected 36 of these forest patches (0.4 to 311 ha, SE = 12.57) which were accessible to the observers in preliminary field visits. Forest patches were also selected so that a minimum distance between them was 2 km to ensure independence in the landscape characteristics surrounding each one.

We used a multi-scale approach (Wiens 1989, Wiens 1994, Andrén 1994, Jokimaki and Huhta 1996, Saab 1999, Drapeau et al. 2000) to assess the independent effects of landscape structure (composition and configuration) and patch characteristics from local habitat effects (structure and floristics) on forest bird occurrence. Bird occurrence was measured by means of census point counts at the selected forest patches. We located one census point in the centre of each forest patch, in which we also measured local vegetation characteristics (local scale). Then the spatial characteristics of the forest patch (forest patch scale) in which the bird point count was located were measured. And finally, we also measured the landscape structure (landscape scale) in 4 km^2 (2 x 2 km) squares centred at each of the bird point counts conducted. Using this method we are able to assess how bird occurrence was related to the characteristics of the surrounding habitat at increasing spatial scales.

Bird censuses

The point-count method (Bibby et al. 1992) was used to determine the species that breed in the forest patches (for similar procedure see Jokimäki and Huhta 1996, Saab 1999). We conducted two bird censuses in each forest patch during the breeding season in 2000, the first from March to April and the second from May to July. The presence of species within a 50-m radius of the count station was recorded during 20 minutes. The census time was long to maximise the probability of detecting breeding bird species (Drapeau et al. 1999). Censuses were made in the period of maximum bird activity, from dawn to 3 hours later, and they were not conducted in adverse weather conditions such as rain or strong wind.

Raptors, owls and nightjars were not reliably detected with our census technique (Bibby et al. 1992) and were therefore excluded from the analyses. Some of the species detected did not breed at all in the fragments, either because they nested in open areas and visited forests only occasionally, or because they were late-season migrants that did not breed in the area. Some other species records from the smallest fragments could be attributable to transient individuals breeding in some other forested areas nearby (Hinsley et al. 1995, Díaz et al.1998). To avoid this potential bias, such records were considered only when direct breeding evidence was obtained in the forest fragment (e.g. nest construction or provisioning behaviour) or when the species was detected on two visits (for a description of a similar procedure see Díaz et al.1998).

Monitoring specific preferences in habitat use is most revealing if birds are grouped by habitat use strategies (Järvinen and Väisäsen 1979). Mediterranean forests usually have a developed shrub layer, which implies that a significant proportion of Mediterranean bird species is adapted to shrubby forests (Tellería and Santos 1999). Another common feature of Mediterranean forests is a high degree of heterogeneity and habitat variation from which generalists or ubiquitous species benefit (Blondel and Aronson 1999).

According to specific dependence on forest habitats for breeding and foraging activities described in the literature (Perrins 1998), we classified the species into two main groups: forest species (species that require forest habitat for both breeding and foraging) and ubiquitous species (species that can use alternative habitats, such as open fields for foraging or breeding). Forest species were in turn grouped into canopy and understorey species, depending of the forest stratum in which they concentrate their activity. Thus, among the canopy species we included tits, arboreal warblers such as the *Phylloscopus bonelli* and *Regulus ignicapillus*, and *Certhia brachydactyla*. Among understorey species we included *Troglodytes troglodytes.*, thrushes such as *Turdus merula* and *Luscinia megarhynchos*, and shrubby warblers such as *Sylvia melanocephala* and *Hyppolais polyglotta*. Finally, among the ubiquitous species we included birds such as *Lullula arborea*, *Muscicapa striata*, pigeons, finches and buntings. Woodpeckers such as *Picus viridis* and *Jynx torquilla* were included in this latter group because in the Mediterranean these species are not only found in forests but also in almond or olive tree crops, and in isolated burnt trunks (Table 1).

Table 1. The bird species found breeding in Aleppo pine forest stations in the study area. Species were classified as canopy (CA), understorey (UN) and ubiquitous (UB) according to their ecological preferences during breeding season. The percentage of counting stations where each species was found is also shown.

Bird species	Ecological Group	% Stations occupied
Lullula arborea Woodlark	UB	22.2
Columba palumbus Wood pigeon	UB	72.2
Streptotelia turtur Turtle dove	UB	33.3
Cuculus canorus Common cuckoo	UB	41.7
Jynx torquilla Wryneck	UB	8.3
Picus viridis Green woodpecker	UB	27.8
Troglodytes troglodytes Wren	UN	58.3
Eritacus rubecula Robin	UN	33.3
Luscinia megarhynchos Nightingale	UN	55.6
Turdus merula Blackbird	UN	88.9
Turdus viscivorus Mistle thrush	UB	2.8
Hyppolais polyglotta Melodious warbler	UN	11.1
Sylvia cantillans Subalpine warbler	UN	2.8
Sylvia melanocephala Sardinian warbler	UN	100.0
Sylvia atricapilla Blackcap	UN	16.7
Phylloscopus bonelli Bonelli’s warbler	CA	47.2
Phylloscopus collybita Chiffchaff	CA	2.8
Regulus ignicapillus Firecrest	CA	27.8
Muscicapa striata Spotted flycatcher	UB	16.7
Aegithalos caudatus Long-tailed tit	CA	36.1
Parus ater Coal tit	CA	8.3
Parus cristatus Crested tit	CA	66.7
Parus caeruleus Blue tit	CA	13.9
Parus major Great tit	CA	75.0
Certhia brachydactlyla Short-toed treecreeper	CA	63.9
Oriolus oriolus Golden oriole	UB	38.9
Lanius senator Woodchat shrike	UB	19.4
Garrulus glandarius Jay	CA	36.1
Passer domesticus *House sparrow*	UB	11.1
Serinus serinus Serin	UB	77.8
Carduelis chloris Greenfinch	UB	38.9
Carduelis carduelis Goldfinch	UB	36.1
Carduelis cannabina Linnet	UB	2.8
Emberiza cia Rock bunting	UB	8.3
Emberiza cirlus Cirl bunting	UB	13.9
Miliaria calandra Corn bunting	UB	5.6

Local habitat structure and floristics

The floristic and structural features of forests usually synthesise the set of local habitat requisites of forest birds (Robinson and Holmes 1984). Therefore, we sampled the local habitat structure and floristic composition around each bird point count within a 50-m radius around the observer. To characterise habitat structure, we estimated the cover of bare ground, the cover of several vegetation layers (0-0.25 m, 0.25-0.5 m, 0.50-1 m, 1-2 m, 2-4m, 4-8m, 8-16 m, >16m), the maximum vegetation height and the number of adult pines in 100 m^2 as habitat structure variables. Within each vegetation layer, relative cover value was defined as the projection of the foliage volume of the layer on a horizontal plane. This was estimated by comparison with a reference chart, following the procedure described by Prodon and Lebreton (1981).

We also estimated the relative cover of understorey plant species following the same procedure. Plant species were grouped according to the phytosociologic criteria shown by Folch (1986) for the eastern Iberian Peninsula. Four main groups were made. First, plants belonging to secondary low shrubland formations on calcareous soils (*Rosmarino-Ericion*), such as *Rosmarinus officinalis*, *Erica multiflora* or *Ulex parviflorus* .Second, plants belonging to primary dense tall shrublands (*Oleo-Ceratonion*), such as *Olea europaea*, *Pistacia lentiscus, Chamaerops humilis* or *Quercus coccifera*. Third, plants belonging to primary Holm-oak forest (*Quercion ilicis*), such as *Quercus ilex, Rhamnus alaternus or Smilax aspera*. Finally, the fourth group was made up of grasses such as *Brachypodium sp.* or *Ampelodesmos mauritanica*, which are often associated with highly disturbed lands. For each census bird point count, we obtained an abundance index for each phytosociological group by summing the cover of plants belonging to each one

Patch variables

Patch characteristics could influence animal populations in fragmented landscapes (Fahrig and Merriam 1994). To analyse the effects of patch characteristics on bird assemblages, we used digitised aerial photographs (1:20000) to construct IDRISI image files using the program MiraMon GIS (Marcer and Pons 1998). The images were then analysed with FRAGSTATS Software (McGarigal and Marks 1995) to obtain patch metrics. Forest shape measures the perimeter^2/size ratio of a particular patch, high values of the index being those that correspond to irregular forest shapes. Core area is defined as the area within a patch beyond a given distance from the edge. In this study, following Murcia (1995), we considered that the distance from the edge to avoid their influences for forest bird species was 50 m and accordingly, FRAGTATS calculated the core area of each forest patch. In addition, total patch size (ha), patch perimeter (m) and distance to nearest forest were also calculated.

Landscape variables

The landscape around each focal patch was quantified in 2 x 2 squares km, so that each the bird point count was located in the centre of the square. This spatial scale has been previously used to study associations between passerine birds and landscape variables (e.g. McGarigal and McComb 1995, Jokimäki and Huhta 1996, Villard et al. 1999). The IDRISI images were analysed with FRAGSTATS Software (McGarigal and Marks 1995) to obtain landscape composition and configuration metrics.

Landscape composition, understood as the spatially non explicit characteristics associated with the presence and amount of different patch types within a landscape (McGarigal and Marks 1995), was assessed by calculating the percentage of six widespread habitat types: burnt short shrublands, burnt tall shrublands, burnt shrublands with isolated pines, Aleppo pine forests, farmland and urbanised areas. The first three habitat types formed the burnt habitat matrix in which forest patches were embedded.

Landscape configuration refers to the physical distribution or spatial character of patches within the landscape (McGarigal and Marks 1995). Due to our interest in bird species associated with forests, we assessed only landscape configuration variables for forests. We selected variables that were known to influence animal distribution (McGarigal and Marks 1995): patch density, edge density, percentage of core forest area in the landscape, mean nearest-neighbour distance between forest patches and nearest-neighbour coefficient of variation. Patch density and edge density were calculated respectively as the number of forest patches and length of forest edges in 100 ha. Forest core area was defined analogously to the patch analysis, that is, as the percentage of forest within the buffer width of 50 m from forest edges, but for the total forest area in each of the 4km^2 landscapes.

Data analyses

The original number of local habitat, patch and landscape variables were separately grouped into a few independent factors using of principal component analysis (PCA) with a varimax normalised rotation. This procedure was established to reduce multicolinearity in the multivariate analysis of bird responses to habitat and landscape characteristics (Hinsley et al. 1995, Díaz et al.1998, Jokimäki and Huhta 1996). The construction of three PCAs emphasises the multi-scale approach: the first analysis for local habitat (local scale), the second for patch (forest patch scale) and the third for 4km^2-landscape metrics (landscape scale). Structure and floristics were included in the same PCA because we considered that birds are influenced by them simultaneously. For the same reason, composition and configuration variables were included simultaneously in the PCAs performed for 4km^2-landscape metrics.

The analysis of animal assemblages in relation to distinct scale patterns requires the control of the effects exerted by the variables of each scale, since they can be correlated. This could be done a priori, with an experimental design that controls the variation of one or two of the scales (Donovan et al. 1997), but this is not always feasible in real landscapes (Drapeau et al. 2000). Therefore, we decided to control *a posteriori* for the effect of including variables at different scales by progressively removing the effect of smaller scale variables. Thus, a backward step-wise multiple regression (Crawley 1993) using a hierarchical approach was used. We conducted three different steps, using at each step the residuals obtained from the best model of the former step. In the first step, the number of species was taken as a dependent variable and local habitat factors as predictors. In the second step, we used the residuals of the former analysis as dependent variable and patch factors as predictors. Finally, in the third step, the residuals of the second regression and landscape factors were used as dependent variables and predictors, respectively. The step in which each set of variables was entered into the model was based on a hierarchical approach considering nested spatial scales at different steps. Assuming that shared variation explained by different spatial scales is likely to be linked with the one operating at the smallest scales, we considered that breeding bird occurrence was affected first by the local habitat, then by forest patch characteristics and finally by landscape surroundings. This method represented a conservative approach with respect to the effects of patch and landscape, but we think that it is necessary if we want to identify the role of large spatial scales on bird distribution. The analyses were performed separately for the number of canopy, understorey and ubiquitous species. All statistical analyses were run with Statistica Statsoft, Inc 1999.

RESULTS

Habitat and landscape PCAs

The principal component analysis conducted with local habitat variables (structure and floristics) gave in five main factors, which accounted for 75.6 % of the variance contained in the original data set. The first factor obtained in this PCA (Quershrub) represented at the same time a gradient of shrub structure and abundance of *Quercion* *ilicis* plants; the second (Amax), a gradient of vertical tree development; the third (Pinedens), a gradient of tree density; the fourth (Lowshrub), a gradient of cover of plants from 25 to 50 cm; finally, the fifth (Talltree) segregated the few point counts with very tall trees. (Table 2).

Table 2. Variables describing the habitat structure in the census station and the factor loadings of each individual variable in the four first factors obtained in the principal component analysis (factor rotation: varimax normalised).

Variable	Quershrub	Amax	Pinedens	Lowshurb	Tall tree
Number of adult pines / 100 m^2	-0.16	0.12	0.86***	-0.13	0.00
Maximum vegetation height	0.27	0.76***	-0.15	0.15	0.28
Cover of bare ground	-0.09	-0.07	-0.19	-0.09	-0.04
Cover of shrubs and grasses less than 25 cm tall	-0.17	-0.06	-0.19	0.05	0.10
Cover of shrubs and grasses from 25 to 50 cm tall	0.02	-0.05	-0.06	0.94***	0.12
Cover of shrubs and grasses from 50 cm to 1 m tall	0.77***	-0.11	0.25	0.22	0.20
Cover of shrubs and grasses from 1 m to 2 m tall	0.89***	0.12	0.08	-0.06	0.23
Cover of shrubs and trees from 2 m to 4 m tall	0.77***	-0.01	0.11	0.00	0.24
Cover of trees from 4 m to 8 m tall	0.39*	0.04	0.79***	0.06	0.10
Cover of trees from 8 m to 16 m tall	-0.04	0.88***	0.26	-0.17	-0.01
Cover of trees more than 16 m tall	0.24	0.13	0.06	0.12	0.93***
Grasses	-0.42*	0.19	-0.20	0.12	-0.17
Species from *Rosmarino-Ericion*	-0.16	-0.18	0.12	0.02	-0.06
Species from *Oleo-Ceratonion*	0.25	0.10	0.04	0.34*	-0.09
Species from *Quercion ilicis*	0.90***	0.14	-0.16	0.02	-0.11
Eigenvalues	4.40	2.50	1.86	1.50	1.08
% Variation explained	29.4	16.7	12.3	10.0	7.2

*** P < 0.001, ** P < 0.01, * P < 0.05.

Three factors, which accounted for 99.3% of total data matrix variance, were obtained from the PCA performed with the variables that described the characteristics of the forest fragments where the bird census point counts were situated (Table 3). The first factor (Fragsize) represented forest size and total core area, the second factor (Fragisolat) was a gradient of fragment isolation and the third factor (Fragshape) determined a gradient from regular to irregular fragment shapes, that is to say, from low perimeter^2/size rates to high ones.

The first five component loadings for 4-km^2 landscape composition and configuration variables accounted for 85.3 % of the variance contained in the original data set (Table 4). The first factor in this PCA (Edgeland) represented a gradient of forest edges in the landscape, which were also positively related to the cover of urbanised areas, and negatively to the cover of low shrublands. The second factor (Pineland) represented a gradient from landscapes dominated by large pine forest tracts to landscapes with many forest patches but low total forest cover. The third (Farmland) and fourth factors (Tallshrubland) determined the cover of farmland and the cover of tall shrublands, respectively. Finally, the fifth factor (Isolpineland) determined the abundance of shrublands with isolated pines.

Table 3. Variables describing the composition and configuration of the pine forest fragment where the census station was situated and factor loadings of each individual variable in the first three factors obtained in the principal component analysis (factor rotation: varimax normalised).

Variable	Fragsize	Fragisolat	Fragshape
Forest Size	0.97***	0.12	0.19
Forest Perimeter	0.82***	0.12	0.54**
Shape Index	0.21	0.13	0.97***
Core Area	0.98***	0.11	0.11
Near Neighbour Distance	-0.13	-0.98***	-0.13
Eigenvalues	3.31	0.92	0.73
% Variation explained	66.2	18.5	14.6

****** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.***

Table 4. Variables describing landscape composition and configuration in the landscape surrounding the census station (4 km^2) and the factor loadings of each individual variable in the first five factors obtained in the principal component analysis (factor rotation: varimax normalised).

Variable	Edgeland	Pineland	Farmland	Tallshrubland	Isolpineland
Burnt short shrublands in 4 km^2	-0.72***	0.57**	-0.12	0.16	-0.25
Aleppo pine forests in 4 km^2	0.62**	-0.73***	0.07	0.12	0.08
Burnt shrublands with isolated pines in 4 km^2	0.20	0.05	-0.21	0.06	0.91***
Burnt tall shrublands in 4 km^2	0.03	0.21	-0.09	-0.95***	-0.05
Farmland in 4 km^2	0.16	-0.02	0.91***	0.11	-0.21
Urbanised areas in 4 km^2	0.74***	0.03	-0.38	0.25	-0.36
Patch density (PD)	0.30	0.89***	0.03	0.02	0.03
Edge density (ED)	0.83***	0.10	0.07	0.01	0.22
Forest core area in the landscape (C%LAND)	0.53*	-0.78***	0.06	0.13	0.05
Mean of near neighbour distance (MNN)	-0.71***	0.02	-0.21	0.10	-0.10
Coefficient of variation of near neighbour distance (NNCV)	0.04	0.80***	0.00	-0.26	0.13
Eigenvalues	4.02	2.25	1.25	0.99	0.86
% Variation explained	36.6	20.5	11.4	9.0	7.8

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Bird species and their associations with habitat and landscape factors

A total of 36 breeding bird species were recorded during the fieldwork (Table 1). The average number of bird species per point count was 12.3 (SD 3.7), while the minimum and maximum values detected were 1 and 18 species respectively. Of these 36 species, 18 were forest species (50%) (10 canopy species and 8 understorey species) and 18 (50%) ubiquitous species.

Canopy species were less affected by local habitat (22.5 % of total variance explained by these factors) than by patch and landscape (35.4 % of total variance explained by these factors) (Table 5). Within the local habitat variables, canopy species were only positively related to the vertical tree development (Amax). Once this local habitat factor was controlled for by using the residuals of the former regression model, fragment characteristics, which accounted for 29.1% of total variance, were the most important predictors for canopy species occurrence. Fragment size, core area and fragment perimeter (Fragsize) (6.3% of total variance) were positively associated with canopy species. But, more interestingly, forest shape (Fragshape) accounted for 22.8% of total variance, irregular shapes being positively associated with these species. After controlling for the smaller scales, the fourth factor of the PCA (Tallshrubland) was the only that entered into the model and the relationship between the cover of tall shrublands and the number of canopy species was positive.

Table 5. Hierarchic three -step multiple regression models. Step 1: number of canopy species as dependent variable and local habitat factors as predictors; Step 2: the residuals of the former analysis as dependent variables and fragment factors as predictors; Step 3: the residuals of the second analysis as dependent variables and landscape factors as predictors. For each step, a backward stepwise regression (P-to-enter=0.05, P-to-remove=0.10, n=36 stations) was used. The explained variation of each step was calculated with respect to the initial dependent variable (species group), not for the residuals. Results are given for canopy, understorey and ubiquitous species.

		Coefficient	F	P	Explained variation
Canopy species					
Step 1: Local habitat					
	Amax	1.03	9.88	<0.01	22.5%
Step 2: Fragment					
	Fragsize	0.54	4.25	<0.05	6.3%
	Fragshape	1.04	15.54	<0.001	22.8%
Step 3: Landscape					
	Tallshrubland	-0.53	4.62	<0.05	6.3%
Model					57.9%
Understorey species					
Step 1: Local habitat					
	Quershrub	1.14	30.57	<0.001	47.3%
Step 2: Fragment					
	Fragsize	0.52	8.28	<0.01	8.8%
	Fragshape	0.31	3.05	<0.1	3.3%
Step 3: Landscape					
	None				
Model					59.4%
Ubiquitous species					
Step 1: Local habitat					
	Quershrub	-0.99	4.75	<0.05	12.2%
Step 2: Fragment					
	None				
Step 3: Landscape					
	None				
Model					12.2%

In contrast with canopy species, species of the understorey were more affected by local habitat factors than by patch features (47.3% vs. 12.1% of total variance, respectively) (Table 5). Understorey species were highly related to local habitat characteristics, specifically with the cover of shrubs from 0.5 to 4 m tall and the abundance of *Quercion ilicis* plants (Quershrub). Fragment characteristics were included in the model, but the overall percentage of explained variation was almost three times lower than in canopy species. As the canopy species, the understorey species were also positively affected by fragment size (Fragsize) and by fragment shape (Fragshape), although only marginally for this latter factor. At a landscape scale, no factor entered into the model after controlling for the effect of smaller scales.

The best model performed with ubiquitous species only accounted for 12.2% of total variance (Table 5). Only local habitat entered into the model of these species, which were negatively related to the presence of shrubs and *Quercion ilicis* plants (Quershrub).

DISCUSSION

Importance of local habitat factors

Our results showed that local habitat features affected bird occurrence in all groups. Tree vertical development was positively related to canopy species, whereas variation in pine density did not affect them. A similar relationship was found in Aleppo pine forest fragments surrounded by a farmland matrix, where forest species as a whole were positively associated with tall trees (Brotons and Herrando 2001). In Aleppo pine forests of SE Spain, López and Moro (1997) showed that, while tall trees favoured forest species, pine density was not positively associated with any of these species. Therefore, as suggested by our studies and by these authors, management practices to reduce tree densities and favour tall pines would benefit forest species. It is especially interesting reporting that, in dry Aleppo pine forests, the selective thinning and pruning can simultaneously contribute to reduce pine density and increase the mean height of trees (Pastor-López 1995).

Understorey species were highly associated to the cover of shrubs and plants associated with Holm oak forests. López and Moro (1997) also found that Holm oaks and associated plant species appeared to be the main determinant of bird community composition and species richness in Aleppo pine forests. In our study area, the presence of Holm oaks implied mixed forests, with pines protruding from these oaks. This probably favoured also canopy birds that in the Iberian Peninsula prefer these broad-leaved trees, such as *Parus major, Parus caeruleus* or *Aegithalos caudatus*, but did not decrease opportunities for those which prefer coniferous, such as *Parus cristatus* or *Certhia brachydactyla* (Tellería and Santos 1995). Moreover, greater arthropod availability in these oaks compared with Mediterranean pines (Illera and Atienza 1995) may greatly enhance the populations of these broad-leaved tree dependent species, which implies an overall increase in forest bird species per point count. However, although the cover of shrubs and plants associated with the Holm oak exerted a positive effect on understorey species, it had a negative effect on ubiquitous species, within which there are no foliage-dwelling species that regularly use food sources located in trees (Perrins 1998). Therefore, the elimination of the understorey would influence negatively understorey species but positively ubiquitous species. Nevertheless, considering that the percentage of variation explained by these plants is higher in the model performed for understorey species than in that for ubiquitous species, hypothetical management practices in this direction would probably result more negative for understorey species than positive for ubiquitous.

Relevance of fragmentation effects

Patch and landscape characteristics play a determinant role in breeding forest species occurrence in forests that are highly fragmented by wildfires. Several studies carried out in fragmented temperate regions have also reported that this type of variables accounted for a significant proportion of the total variance in forest bird occurrence, ranging from 20% to 50% (e.g. Pearson 1993, Jokimäki and Huhta 1996, Drapeau et al. 2000, Pino et al. 2000). Therefore, although some of these studies could show landscape effects that might be in fact due to correlations between these and local habitat characteristics, on the whole, these results suggest that models of bird occupancy solely based on habitat characteristics could be misleading in fragmented landscapes.

Studies on the effect of fragmentation on birds have usually found a positive relationship between fragment size and the number of forest bird species (e.g. Bellamy et al. 1996, Díaz et al. 1998, Tellería and Santos 1997), which denotes the importance of habitat loss in structuring bird communities in fragmented woodlands. We also found a significant role of forest size in forest species, the larger forest fragments being those that maintained richer forest bird communities. The fact that, in our study case, bird richness in equal sized bird point counts was dependent on size can be associated with two non-exclusive possible explanations. On one hand, very small forest patches may have not met minimum area required for some forest species and therefore, these species may be absent from the point counts located within those patches. On the other hand, the independence between size and other analysed variables such as isolation and forest shape also suggest that the habitat diversity hypothesis in relation to forest size (Berg 1997) may be an alternative explanation behind the positive relation between bird richness and patch size. Furthermore, the relationship between forest bird richness and the size and configuration of forest patches indicates that bird assemblages in our forest mosaics did not fit the random sample hypothesis (Connor and McCoy 1979).

A spatial consequence of habitat fragmentation is the isolation of remnant patches of habitat. This study did not show any effect of isolation on species presence, which contrasts with other two studies carried out in Iberian pine forests patches, in which isolation played a significant role in bird assemblages (Díaz et al. 1998, Brotons and Herrando 2001). The importance of isolation differed in these two studies, since its effect was higher in the first (where the forest patches were surrounded by cereal croplands) than in the second (where the forest patches were surrounded by vineyards). In our case, we did not find effects of isolation in landscapes where the matrix was essentially a mosaic of burnt shrublands, thus suggesting that the forest fragmentation provoked by fires does not seem to isolate bird populations. All these results seem to indicate that the matrix type could be involved in the isolation of the forest fragments and thus in the composition of their bird assemblages (Mönkkönen and Reunanen 1999). However, in another study carried out in Iberian oak forest patches surrounded by cereal crops, Tellería and Santos (1999) found a lack of effect of isolation on bird species occurrence. Therefore, even on a regional scale (e.g. the Mediterranean Iberian Peninsula), current knowledge is not sufficient to generalise about the role of isolation, thereby highlighting the relevance of the landscape context in predicting the effects of fragmentation on wildlife.

We found that forest species richness was highly favoured by irregular forest shapes (high perimeter^2/size rates). This result suggests some positive effects of the length of edges for Mediterranean forest birds. However, forest edges have been commonly presumed to have deleterious biotic and abiotic consequences for the organisms that inhabit forests fragments (Murcia 1995). Within the negative biotic impacts, nest predation and brood parasitism may affect forest birds and, in highly fragmented forests, these impacts could be so high that nesting birds cannot fledge young enough to maintain stable populations (Donovan et al. 1995). In England, Hinsley et al. (1999) reported that the breeding performance of *Parus major* and *Parus caeruleus* declined as fragmentation increased. With regards to abiotic edge effects, Dolby and Grubb (1999) showed that strong winds and low temperatures affected negatively bird populations inhabiting highly fragmented temperate woodlands. In spite of the data suggesting negative edge effects for birds, Friesen et al. (1999) found that the distance from nests to the nearest forest edge did not significantly affect the nesting success of several Canadian forest bird species. Furthermore, Santos and Tellería (1992) found that Mediterranean forest patches differ from the usual pattern of nest predation found in other fragmented landscapes. These authors studied edge effects on predation of artificial avian nest in a forest archipelago situated in an agricultural area of Central Spain and found a trend towards lower predation on the forest edge than in the interior. Moreover, Tellería and Santos (1992) reported for the same trail, a tendency of predation to increase as forest size class decreased. Therefore, in the Iberian Peninsula, available data suggest that forest edges do not lead to an increase in nest predation but small forests do. Our results are consistent with this suggestion since, on one hand, fragment size was positively related to the richness of forest species and, on the other, high perimeter^2/size rates positively influenced forest bird occurrence. Understorey species were less strongly related to forest shape than canopy species probably because birds that inhabit the shrubby understorey do not perceive edges between shrubby pine forests and shrublands as canopy species do.

Indeed, food availability may be another important factor behind positive boundary effects. Edges may have higher arthropod availability than forest interior (Jokimäki et al. 1998), which represents a positive edge factor for most forest birds with regard to the main food supply during the breeding season. Furthermore, Forman (1995) showed that curvilinear boundaries and amoeboid shapes, such as those typically provoked by forest fires (see Chuvieco 1999 for data about the complex forms provoked by fire in Eastern Spain), facilitated animal movements towards the immediate surroundings and provided new microenvironments. This author also suggested that this permeability may also be enhanced by low edge contrast in forest-shrubland boundaries compared with those of forest-farmland or forest-urbanised areas. Therefore, although edges are often considered as negative for forest birds, our results support the rejection of such generalisations and show positive edge effects in particular landscapes.

In summary, our initial hypothesis that, apart from habitat loss, fire-related fragmentation has a low impact in Mediterranean forest species can be confirmed since no negative effect was detected for isolation, and positive perimeter/size effects were observed for these species. As suggested by Tellería and Santos (1999), this seems to indicate that Mediterranean forests have been historically so heavily affected by fragmentation that interior forest birds are now very scarce or extinct and remaining species are well adapted to these heterogeneous landscapes (see also Mönkkönen and Welsh 1994 for similar processes in boreal forest mosaics).

Our analyses also showed that the contribution of patch and landscape differed a lot depending on the ecology of each group studied. Within forest birds, understorey species were much less influenced by fragment and 4km^2-landscape characteristics than by local habitat, whereas the relationship was opposite for canopy species. This difference suggests that the fragmentation associated with fire regime may affect more strongly canopy than understorey species. For this last group, the resulting shrubby matrix does not differ much from their preferred habitat type, and hence, probably perceive a much less fragmented landscape than canopy species do.

The model for ubiquitous species, which had much less predictive power than those of forest species, did not include any patch feature. This result contrasts with other studies carried out in farmlands, which showed that this group of species, sometimes called edge species, was related to fragmentation variables, especially to forest edges (Bellamy et al. 1996, Jokimäki and Huhta 1996). Hence, it is possible that in the burnt areas, ubiquitous species do not respond to the landscape and patch variables as they do in farmlands and that other unanalysed landscape features have a greater relevance than the commonly analysed forest edges. Forman (1995) reported that ubiquitous species usually tend to concentrate in abrupt edges, such as those between grasslands and forests. Sisk et al. (1997) found in Mediterranean patchy woodlands of California that the occurrence and abundance of ubiquitous bird species were higher in forest fragments surrounded by grassland in those surrounded by shrubland. Hence, we suggest that the soft edge between the shrubby matrix and the remaining forest patches does not provide a suitable habitat for most of these species.

Landscape scale

We found few landscape effects after controlling for the effect of smaller spatial scales. Probably the most relevant result was that the cover of forest in the landscape was not relevant for any group of birds, which is consistent with the absence of any effect of patch isolation. Therefore, these results suggest that the shrubby matrix is highly permeable for birds.

The only landscape variable that affected birds was the cover of tall shrublands in the 4-km^2 landscape, and only for the group of canopy species. It is quite surprising that these birds were not affected by the proportion of forests in the landscape but were positively affected by that of tall shrublands. The previously mentioned lack of associations between all forest species and patch isolation suggests that tall shrublands do not favour canopy species by enhancing landscape connectivity but rather by increasing habitat quality in forests surrounded by this type of vegetation. Hence, we believe that canopy species, which are clearly benefited from high $perimeter^2$/size rates and thus seem more attracted than repelled by edges, may go to these adjacent habitats, which can be used as feeding sites by several of these species (Perrins 1998, personal observations). The observation of stable breeding territories of canopy species in very isolated and small forests (we have recorded the breeding of *Certhia brachydactyla* and *Parus major* in forests as small as 0.4 ha) can only be explained by the use of adjacent tall shrublands (habitat supplementation, sensu Dunning et al. 1992). In contrast, understorey species, which in a local scale were highly related to the cover of shrubs, were not related to the cover of tall shrublands in the landscape. This may be also due to an enlargement of niche breadth in this group of birds. However, in this case, understorey species probably use not only tall shrublands but also short shrublands with or without isolated pines. Here, specific relationships between landscape characteristics and occurrence of understorey species may be difficult to reveal due to similar preference of other habitats supplementary to forests.

Conservation implications

The main contribution of this study to the knowledge of the effects of fragmentation on birds deals with the landscape patterns provoked by wildfires in the Mediterranean area. We believe that the data obtained may also represent an appreciable contribution to landscape management, since the importation of guidelines from other regions with different perturbation regimes can be misleading. Thus, several conclusions that may be drawn from a conservational perspective. First, although fires reduce the cover of available habitat for Mediterranean forest bird species, they simultaneously create new landscapes where the remaining forest patches are suitable habitats for these species. Second, forest management is not necessary negative for birds. The concomitant increase of tree height derived from decreasing pine density by selective logging could even benefit forest canopy species, although the maintenance of forest shrubs is essential for understorey species. Third, bearing in mind the fundamental role of patch features for the forest avifauna of these landscapes, actions that consider exclusively local habitat management can be insufficient or inappropriate. As also reported in other fragmented landscapes, patch size plays also a key role for promoting forest birds communities in Mediterranean landscapes. However, patch isolation did not affect bird occurrence and, irregular forest shapes with shrub-forest edge favoured the maintenance of a diverse forest bird community. Suggestions for spatial arrangement of forest patches, traditionally based on minimising perimeter/area rate, should be revised for Mediterranean forested landscapes affected by fires.

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Factors affecting bird communities in fragments of secondary pine forests in the north-western Mediterranean basin[1]

Abstract

We assessed the influence of size, extent of isolation and vegetation structure of secondary forest fragments on the richness and species composition of breeding bird communities in a sample of pine forest fragments surrounded by agricultural matrix in the north-western Mediterranean basin. Fragment size was the main predictor of bird's occurrence, since it accounted for 70 % of the model variation. Isolation was also a valuable predictor of species occurrence, especially for forest specialists. Finally, subarboreal vegetation such as Holm oak and a well-developed tree layer of large pines favoured forest species occurrence. Therefore, in spite of the large history of human impact, forest birds in Mediterranean mosaics are sensitive to both habitat loss and isolation of remnant patches in a similar way to the patterns found in other temperate fragmented landscapes where human impact is more recent.

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[1] With Lluís Brotons. University of Barcelona. Acta Oecologica (2001)

INTRODUCTION

Mediterranean habitats have been largely exploited by human activities and land use modification has affected the landscape configuration for a long time. Because of exploitation and substitution for agriculture terrain, original Mediterranean forests have widely disappeared and a secondary, fragmented landscape mosaic has dominated the Mediterranean basin for many centuries (Blondel & Aronson 1999).

In agricultural areas, forest bird diversity is usually maintained in secondary forest fragments isolated to a variable extent. In large areas of the Iberian Mediterranean coast, only such secondary forest fragments of the original forest cover remain, and persistence of forest bird metapopulations relies on their vegetation structure and spatial arrangement (Opdam 1991, Tellería & Santos 1994, Hanski 1999). These fragments, usually dominated by Aleppo pine, are usually surrounded by a shrubby or agricultural matrix and are subjected to management, which is rarely aimed at increasing present or future biodiversity. The forest management policy rather points towards a clearing of the understory in order to reduce the amount of accumulated matter, which is thought to reduce the risk of forest fires and favour the growth of the tree layer (Vélez 1990, Pastor-López 1995). This will probably have considerable impact on bird assemblages but so far bird communities inhabiting these secondary forests have received little attention (López & Moro 1997).

The spatial arrangement of forest patches is an important determinant of bird community structure. Much is known on the effects of fragmentation on birds of boreal and temperate forests. This includes a decrease in the number of birds due to pure habitat loss and to the indirect effects of fragmentation such as increased nest predation and isolation (Opdam *et al.* 1985, Wilcove 1985, Blake & Karr 1987, Saunders *et al.* 1991, Haila *et al.* 1993, Hinsley *et al.* 1995, Hinsley *et al.* 1996, Villard *et al.* 1999). However, the impact of these factors in present Mediterranean landscape mosaics remains largely unknown (Santos & Tellería 1992, Tellería 1992, Farina 1997, Díaz *et al.* 1998, Tellería & Santos 1999).

So far, no attempt has been made to study the factors that determine bird assemblages in highly fragmented Aleppo pine plantations. Assessing the independent effects of the spatial arrangement and vegetation structure on birds occurrence and distribution on suitable fragments of secondary pine forest is an essential tool for present habitat managing (Díaz *et al.* 1998). Here, the influence of size, level of isolation and vegetation structure of forest fragments on the richness and species composition of the breeding bird communities they support were independently analysed in a sample of pine forest fragments surrounded by agricultural matrix in the north-western Mediterranean area.

METHODS

Study area

Field work was carried out in the Penedes area (Figure 1) in the northeast of the Iberian peninsula (45 80 N, 3 90 W, 100 m a.s.l.). This zone is heavily cultivated, with vineyards dominating areas where the Holm oak (*Quercus ilex)* forest has been almost completely eliminated. Secondary forest fragments of varying size dominated by Aleppo pine (*Pinus halepensis)* can now be found among vineyards in patches not appropriate for farmland. Larger extensions of Aleppo pine forests affected to a variable extent by forest fires and exploitation are also found in the mountain ranges surrounding the Penedes plain.

We sampled 43 forest fragments with sizes ranging from 0.1 to 8000 ha (table 1). We included all the large forest fragments within the Penedes plain and three large continuous pine forests located at the surrounding uncultivated area nearby. The size of each fragment, as well as the distance to the nearest continuous forest (which could stand as 'sources' of dispersing individuals) was measured on aerial photographs. The distances measured were the linear distances between the edge of each forest fragment to the nearest edge of a large continuous forests (>100 ha). Forested narrow stripes following small rivers are common in the area and they are likely to be used as potential dispersing corridors by birds. Because of its interest, we also measured the linear distance of each forest fragment to the nearest riparian habitat corridor.

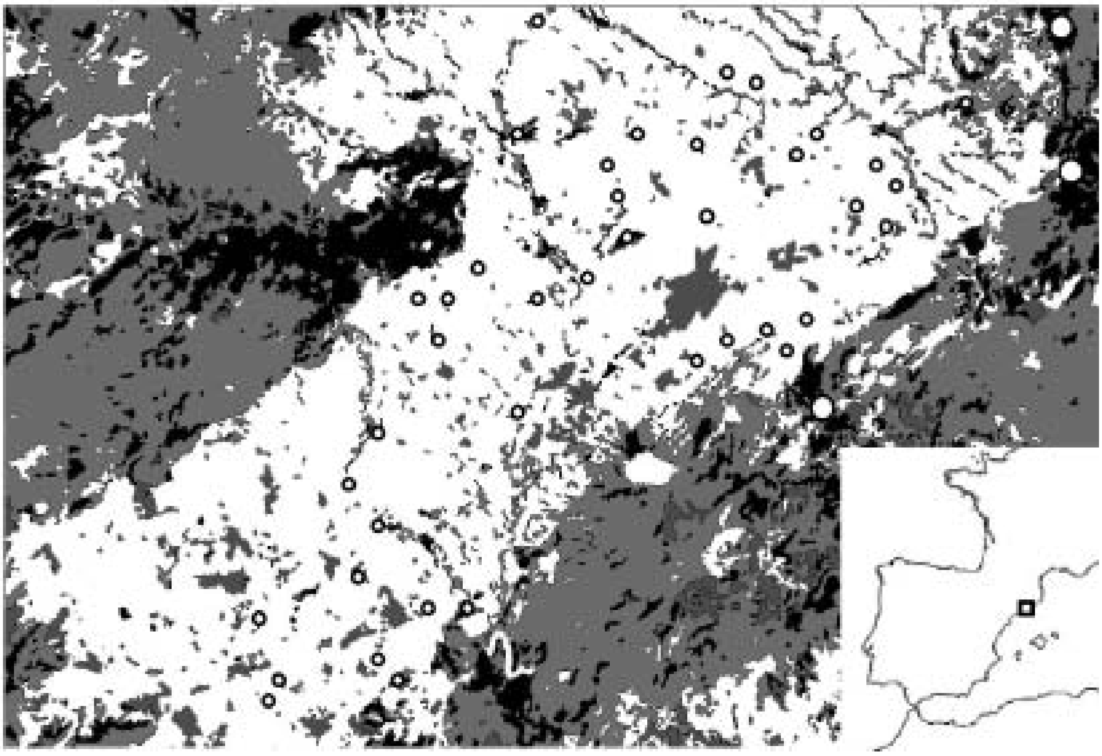

Figure 1. Land-use map of the study area in 1992 containing the Penedes plain (in the centre) and surrounding, less humanized areas. Black areas represent forests, grey areas, shrubby vegetation or urban areas in the plain. White areas represent agriculture. The small circles show the locations of the forest fragments in the plain whereas the large circles show the large forests investigated in the nearby areas.

Bird censuses

We conducted bird censuses in each fragment during the 1999-breeding season (April-July). We recorded the presence/absence of each bird species in two to four visits to each fragment on average, evenly distributed through the period studied (see Hinsley *et al.* 1996, Díaz *et al.* 1998 for similar procedure). We did not attempt to measure the abundance of breeding birds since comparisons of abundance estimates between habitat patches of highly different sizes are misleading (reviewed by Haila 1988, Opdam 1991).

Censuses were made early in the morning and late in the afternoon in order to avoid central hours of the day, when bird activity is at its minimum. We noted the presence of every bird species as well as any sign of breeding activity within the forest fragment (singing males, territorial behaviour, nest construction or provisioning, etc). Small to medium size forest fragments (0.1-30 ha) were searched by walking a route established to get within 100 m of every point in the forest fragment in each visit (Sutherland 1996). Along the routes, we noted all the birds contacted and the results from all the visits were pooled together. The duration of routes was established according to the size of the forest fragment and ranged from 30 min to 2 hours in the larger fragments. The first visit to each fragment accounted for 95% of the total species recorded. Therefore, we made sure that the list of species listed for each fragment was complete and no missing species were left out. The largest fragments (>30 ha) were also censused by means of repeated point counts distributed across the whole area of study. In the largest forests (>100 ha) surrounding the Penedes plain, we estimated the density of each species using point counts with several counting bands (Bibby *et al.* 1992). In addition to presence/absence data, an estimate of the regional abundance (number of birds per 10 ha) of each bird species was thus obtained. Both routes and point counts were established to sample the edges and the interior of each forest fragment.

Raptors, except Sparrowhawk (*Accipiter nisus)* (a species closely linked to forested habitat), owls and nightjars, were not reliably detected with our census technique and so were excluded from the list of breeding species. Some of the species detected did not breed at all in the fragments studied, either because they nested in open areas and visited forests only occasionally (Bee-eater, *Merops apiaster;* aerial feeders such as swallows, swifts), or because they were late-season migrants that did not breed in the area studied (Pied flycatcher *Ficedula hypoleuca*). Some species records from the smallest fragments (<1 ha) could be attributable transient individuals breeding in some other forested areas nearby (Hinsley *et al.* 1995, Díaz *et al.* 1998). To avoid this potential bias, such records were considered only when we obtained direct evidence for breeding in the fragment (e.g. nest construction or provisioning behaviour) or when we detected the species in at least two visits.

We classified the species found into three groups according to their dependency on forest habitats during breeding following Díaz *et al.* (1998) (Table 1). (i) Ubiquitous species, such as pigeons, sparrows and some finches, are able to nest and feed in other habitat types other than the forest (e.g. isolated shrubs, field margins or even croplands). (ii) Forest generalists, such as thrushes, some corvids and most finches, breed in forest but can also exploit the agricultural matrix surrounding them. Most forest generalist species are tree- or shrub –nesters and ground feeders. (iii) Forest specialists, such as most warblers and pariforms (tits and allies), are restricted to forest habitats for nestling and feeding. They place nests on trees and shrubs, and forage in tree and shrub canopies as well as on tree trunks and branches.

Table 1. The bird species found breeding in Aleppo pine fragments in the Penedes area. Species were classified as ubiquitous (U), forest generalist (G) and forest specialists (S) according to their dependence on forest habitats during breeding. The number of fragments where each species was found (from a total of 43 fragments), the size of the smallest forest fragment where the species was found and its regional density (based on point counts made in continuos forest areas of the region) are also shown.

Bird species	Group	No of fragments occupied	Smallest fragment	Regional density
Alectoris rufa (Alru) Red-legged partridge	U	3	3.3	0.10
Accipiter nisus (Acni) Sparrowhawk	S	3	11.1	0.10
Columba palumbus (Copa) Wood pigeon	U	32	0.1	1.35
Streptotelia turtur (Sttu) Turtle dove	G	9	0.4	1.04
S. decaoto (Stde) Mourning dove	U	1	0.5	0.10
Cuculus canorus (Cuca) Common cuckoo	G	2	875	0.12
Upupa epops (Upep) Hoopoe	U	15	0.5	0.10
Picus viridis (Pivi) Green woodpecker	G	5	1.2	0.30
Eritacus rubecula (Erru) Robin	G	12	1.1	0.26
Luscinia megarhynchos (Lume) Nightingale	G	27	0.1	1.32
Turdus merula (Tume) Blackbird	G	18	0.1	1.70
T. viscivorus (Tuvi) Mistle thrush	G	1	0.6	0.10
Cettia cetti (Cece) Cetti’s warbler	U	3	11.1	0.10
Hyppolais polyglotta (Hypo) Melodious warbler	G	2	5.9	0.10
Sylvia melanocephala (Syme) Sardinian warbler	G	39	0.1	15.12
S. atricapilla (Syat) Blackcap	S	6	0.4	0.10
Phylloscopus bonelli (Phbo) Bonelli’s warbler	S	8	1.6	1.15
Muscicapa striata (Must) Spotted flycatcher	S	1	1.6	0.20
Troglodytes troglodytes (Trtr) Wren	S	12	1.1	4.35
Aegithalos caudatus (Aeca) Long-tailed tit	S	11	2.8	1.56
Parus ater (Paat) Coal tit	S	2	875	0.90
P. cristatus (Pacr) Crested tit	S	16	0.5	3.36
P. caeruleus (Paca) Blue tit	S	4	1.2	0.11
P. major (Pama) Great tit	S	31	0.1	1.69
Regulus ignicapillus (Reig) Firecrest	S	10	2.7	4.72
Certhia brachydactlyla (Cebr) Short-toed treecreeper	S	20	0.6	2.78
Garrulus glandarius (Gagl) Jay	G	8	1.2	1.19
Oriolus oriolus (Oror) Golden oriole	G	3	1.8	0.10
Pica pica (Pipi) Magpie	U	39	0.1	0.30
Sturnus vulgaris (Stvu) *Common starling*	U	1	2.7	0.10
Passer domesticus (Pado) *House sparrow*	U	33	0.1	0.10
Serinus serinus (Sese) Serin	U	41	0.1	4.03
Carduelis chloris (Cach) Greenfinch	G	28	0.1	0.18
C. carduelis (Caca) Goldfinch	U	39	0.1	0.31
Emberiza cia (Emca) Rock bunting	U	1	8000	0.20
E. cirlus (Emci) Cirl bunting	U	16	0.1	0.10

Vegetation structure

The vegetation structure of plantations was characterised immediately after bird censuses were completed. The vegetation structure at each forest fragment was measured within a 25 m radius around the centre of the forest fragment. In larger fragments, where birds were censused by means of point counts, vegetation structure was measured at each bird count station and a mean for the fragment was calculated. We estimated the cover of several vegetation layers (0-0.25 m, 0.25-0.5 m, 0.50-1 m, 1-2 m, 2-4m, 4-8m, 8-16 m) and rock layer as habitat variables. These layers were in geometrical progression because of the logarithmic functions found by Prodon & Lebreton (1981) relating bird species and vegetation structure variables. Within each layer, the relative cover value was defined as the projection of the foliage volume of the layer (or rock layer) in a horizontal plane. We estimated this projection by comparison with the reference chart following the procedure by Prodon & Lebreton (1981). According to this method, the observer can reach a reliability of ±10 %. The final number of shrubs and tree cover variables was selected after considering only species covering at least 10 % of the surface in at least 10% of the study sites.

The original number of vegetation variables (Table 2) was summarised into a few independent factors by means of principal component analysis carried out on the average values of each variable for each forest fragment. This procedure was established to reduce multicolonearity in the multivariate analysis of bird responses to forest traits (Hinsley *et al* 1995, Díaz *et al.* 1998).

Data analyses

The possible variables affecting the species richness of breeding birds: size of the fragment, distance to the corridor, distance to nearest continuous forests and vegetation structure, were studied with a step-wise multiple regression (Crawley 1993). The analyses were performed for the total number of species included in the study and for each group separately. The size of the fragment and its distance to the nearest corridor and to the tract of continuous forest was normalised using logarithmic transformations. Vegetation structure for each forest fragment was measured as the factor scores in the three first principal components obtained in the multivariate analysis of vegetation traits described above.

The distribution of individual bird species in fragments was modelled using backward step-wise logistic regressions. This technique estimates the dependency of a binary variable from a set of independent or predictor variables, which can be either discrete or continuous (Hosmer & Lemeshow 1989, see Hinsley *et al.* 1995 for a similar procedure). Here, we estimated the probability of occupancy of forest fragments of each breeding species (1 if occupied and 0 if unoccupied) as a function of the size of the forest fragment, the distance to the corridor and to the nearest continuous forest and their vegetation structure as measured by the first three principal components of vegetation traits. All the species found in less than 5 forest fragments were excluded from our analyses, although this criterion was relaxed to 3 in a few forest specialists because of their particular interest.

We defined occupancy as the proportion of forest fragments occupied by a species from the total pool of fragments, whereas regional density was defined as the density of a species (individuals/10 ha) in a continuous forest habitat (see above).

RESULTS

Vegetation structure

The principal component analysis conducted derived three main factors, which accounted for 51.55 % of the variance contained in the original data set (Table 2). The first (PC1, 24.60% of the variance) was positively correlated with the percentage of vegetation cover in height between 0.5 m and 4 m, and with the cover of subarboreal forest species like Holm oak (*Quercus ilex)* and Spanish oak (*Quercus cerrioides).* Moreover, the concordance of PC1 with humid bushes like (*Hedera helix)* and (*Rubus ulmifolius)* and its disagreement with pine cover suggested that it is an index of subarboreal original vegetation mainly associated with the presence of the Holm oak. The second factor (PC2, 13.62 % of the variance) was negatively related to the percentage of cover by small and medium size pines (2-8 m) and positively associated with the percentage of cover by larger pines (8-16 m). Therefore, negative values in this factor were associated with dense medium-height pine forests with Mediterranean dry vegetation such as the Rosemary (*Rosmarinus officinalis).* The third factor (PC3, 13.33 % of the variance) was positively correlated with the cover of low shrubs (0.25 - 2 m), mainly Lentisk (*Pistacia lentiscus)* and Kermes oak (*Quercus coccifera).* It separated shrubby rich forests from those with less vegetation at lower layers.

Table 2. Variables describing the structure of the vegetation in the plantations studied, and factor loadings of each individual variable in the three first factors obtained in the principal component analysis of the vegetation structure of forest fragments.

Variable	Description	PC1	PC2	PC3
COVER25	Cover of herbaceous plants less than 25 cm tall (%)	-0.35*	0.14	0.16
COVER50	Cover of shrubs from 25 to 50 cm tall (%)	0.03	0.00	-0.85*
COVER1	Cover of shrubs from 50 cm to 1 m tall (%)	0.50*	0.06	-0.78*
COVER2	Cover of shrubs and small trees from 1 m to 2 m (%)	0.79*	0.04	-0.47*
COVER4	Cover of shrubs and trees from 2 m to 4 m (%)	0.62*	-0.39	-0.12
COVER8	Cover of trees from 4 m to 8 m (%)	0.02	-0.73*	0.22
COVER16	Cover of trees from 8 m to 16 m (%)	-0.05	0.84*	0.09
COVER+	Cover of trees above 16 m tall (%)	0.42*	0.28	0.11
PINUS	Cover of Aleppo Pine *Pinus halepensis* (%)	-0.50*	-0.40*	0.14
QILEX	Cover of Holm oak *Quercus ilex* (%)	0.79*	0.25	-0.15
QCOCCIFERA	Cover of Kermes oak *Quercus coccifera* (%)	-0.19	-0.30	-0.54*
QCERRIOIDES	Cover of Spanish oak *Quercus cerrioides* (%)	0.73*	0.00	0.06
PISTACIA	Cover of Lentisk *Pistacia lentiscus* (%)	0.00	-0.13	0.45*
ROSMARINUS	Cover of Rosemay *Rosmarinus officinalis* (%)	-0.26	-0.43*	-0.10
OLEA	Cover of Olive trees *Olea europaea* (%)	-0.02	0.34	0.08
RUBUS	Cover of Blackberry *Rubus olmifolius* (%)	0.73*	0.30	0.07
HEDERA	Cover of Ivy *Hedera helix* (%)	0.63*	-0.14	0.16
	Eigenvalue	3.93	2.17	2.13
	%variance	24.60	13.62	13.33

* $P<0.05$

Vegetation factors were not significantly correlated or only slightly with the spatial factors analysed (Table 3). Only PC3 was related positively related to distance to corridors and negatively to fragment size (Table 3). Therefore, interrelations between vegetation and spatial factors were low enough to assume they do not affect the relative weight of each type of factors on explaining species occurrences.

Table 3. Correlation matrix of spatial (log-transformed) and vegetation factors included in the study. Correlation coefficients are Pearson coefficients. SIZE, fragment size in ha; CORRIDOR, the distance to the nearest corridor in m; CONTINUOUS, the distance to the nearest tract of continuous forest >500 ha in m, and the three multivariate gradients of vegetation structure (PC1, PC2 and PC3).

	CONTINOUS	CORRIDOR	SIZE	PC1	PC2	PC3
CONTINOUS	1	0,40*	-0,68*	0,17	0,06	0,25
CORRIDOR		1	-0,54*	-0,21	-0,05	0,30*
SIZE			1	0,03	-0,08	-0,31*
PC1				1	0,00	0,00
PC2					1	0,00
PC3						1

Bird richness and structure of forest fragments

Overall, 36 species were found breeding in the 43 forest fragments analysed here (Table 1). From these total, 12 (33.3 %) were ubiquitous species; 12 (33.3%) forest generalists and 12 (33.3%) forests specialists.

Total species richness was directly related to the size of the forest fragments, their distance to corridor habitat and to the three factors involved in the description of the vegetation structure (Table 4). The most important factor was fragment size. Specifically, fragment size accounted for around 70 % of variation in forest species richness (Table 4). As a result, fragments of up to 2.0 ha contained only around 30 % of the total number of species, and only fragments larger than 25 ha contained more than 60 % of the total number of species (Table 5). On the other hand, ubiquitous species were much less affected by fragment size compared to forest species (Table 4), and small and large fragments did not differ much in the total number of species of this group (Table 5).

Table 4. Multiple regression models for the concordance between the richness of breeding bird species and forest fragment features; size, distance to corridors, distance to nearest continuous forest and structures of vegetation (n= 43 forest fragments). Results are given for all species combined, and for ubiquitous and for forest species (both generalists and specialists taken separately).

Independent variable	*Coefficient*	*S.E.*	*% variance*	*P*
All species				
Constant	9.14	1.53		<0.001
Fragment size	2.63	0.27	73.73	<0.001
Distance to corridors	-0.30	0.18	1.11	<0.1
PC1	1.04	0.39	3.93	<0.01
PC2	1.095	0.38	4.03	<0.01
PC3	-0.83	0.41	2.21	<0.05
Model			85.01	<0.001
Ubiquitous species				
Constant	3.58	0.22		<0.01
Fragment size	0.35	0.1	27.30	<0.01
PC3	-0.32	0.17	7.71	<0.1
Model			35.01	<0.01
Forest generalists				
Constant	1.96	0.26		<0.001
Fragment size	1.37	0.11	70.05	<0.001
PC1	0.75	0.19	7.38	<0.001
PC2	0.38	0.19	1.96	<0.05
			79.90	<0.001
Forest specialists				
Constant	2.27	0.55		
Fragment size	0.97	0.13	65.32	<0.001
Distance to corridors	-0.24	0.10	7.80	<0.01
PC1	0.33	0.19	1.35	<0.1
PC2	0.55	0.18	4.50	<0.01
			80.02	<0.001

The relative importance of isolation and vegetation structure was different in forest generalists and specialists and almost negligible in ubiquitous species. Whereas the richness of forest generalists was more affected by vegetation structure, namely PC1 and marginally PC2 (Table 4), forest specialists were more heavily influenced by the distance to corridors and only secondarily by vegetation structure (PC2, Table 4).

The large range of sizes included in our analyses did not have a strong impact on the models conducted. When only fragments smaller than 30 ha were included in the regressions (N=38), the final best models for forest specialists (r^2=0.66) and generalists (r^2=0.61), and ubiquitous species (r^2=0.25) remained containing the same significant explanatory factors (Table 4) as the analysis conducted on the complete data set. However, the weight of fragment size in explaining species presence decreased from 70 % to 35 % in forest specialists and from 65 % to 40 % in forest generalists, increasing the weight of the other explanatory factors such as corridor distance (and vegetation structure in forest specialists (28 % of the variation, both factors combined) and vegetation structure for forests generalists (20 % of the model variation).

Table 5. Percentage of breeding forest birds and ubiquitous species maintained by forest fragments of different size. The total number of species was 36, (24 for forest species and 12 for ubiquitous species); the number of fragments for each class size is in parenthesis. A bird species was considered to be maintained by the corresponding size class of forest fragments if more than 20% of fragments within such class were occupied (according to Díaz et al. 1998).

	Size class (ha) *0.1-2.0*	*Size class (ha)* *2.1-25.00*	*Size class (ha)* *25.1-100.00*	*Size class (ha)* >100.0
All species	33.3 %	55.5 %	64 %	86 %
Forest species	27 %	58 %	65 %	92 %
Ubiquitous species	58 %	58 %	58 %	75 %
	(25)	(18)	(3)	(2)

Occurrence of individual bird species

We conducted a logistic regression model for 26 species (Table 6). All but two of the models were significant (<0.05). The model for the Cirl bunting was marginally significant (<0.1) and only for the Serin all the variables were excluded from the full model. These species were both ubiquitous. There was a great difference between the classification efficiency between ubiquitous and forest species. The percentage of occurrences observed that had been correctly predicted by the models was only between 50% and 66% in ubiquitous species, whereas it was much higher, between 63% and 100%, in forest species (Table 6). Our data indicate that with the set of variables used, the overall fit of the models was better in forest than in ubiquitous species.

Fragment size was the main predictor of bird species occurrence. Size was positively correlated with occurrence in 84% of the models including forest species. Furthermore, 21% of the models included size as the only significant predictor. In contrast, fragment size was only included in two out of seven ubiquitous species (28%). This significant relationship was negative for one of the species (the Common sparrow, Table 6).

Isolation of forest fragments was also important for the prediction of species occurrence in these forest fragments. Distance to corridors or to continuous forest habitats was significant in 47% of forest species (26% were related to the distance to corridors and 21% to the distance to continuous forest habitats). Ubiquitous bird occurrence was less affected by fragment isolation, since only 28% of the species model included either the distance to corridors or to continuous habitats (Table 6).

In forest species, floristic composition and vegetation cover were included in 68 % of the models. Overall, the probability of forest bird occurrence increased with the presence of Holm oak and the diversity of subarboreal vegetation (32% of forest species). Furthermore, 30% of species occurrence was favoured by the presence of large pines and therefore a well developed tree layer of adequate height (26 % of forest species). Vegetation structure was also an important predictor in most specific models of ubiquitous species, and 71% of the models contained at least one vegetation descriptor (Table 6).

Table 6. Step-wise logistic regression models (P-to-enter =0.05, P-to-remove =0.10) for the probability of occupancy of forest fragments by each bird species as a function of the size (SIZE, in ha, log-transformed), the distance to the nearest corridor (CORRIDOR, in m, log-transformed), the distance to the nearest tract of continuous forest (>500 ha, CONTINUOUS, in m, log-transformed) and the three multivariate gradients of vegetation structure (PC1, PC2 and PC3) of fragments. Models are of the form: P(occupancy)+ $1/(1+e^{a+b1X1+b2X2+b3X3+b4X4+b5X5+b6X6})$. The percentage of fragments correctly classified as occupied [P(occupancy)>0.5] or unoccupied [P(occupancy)<0.5], as well as the significance level for the whole model, are also shown. See Table 1 for species abbreviations.

Bird Species	Model	Overall model classification (%)	X^2	d.f.	*P*
Acni	-6.11+1.28 SIZE	83.33	13.48	1	<0.001
Alru	-5.23-3.22 PC3	55.15	10.04	1	<0.001
Copa	-1.34+0.44 CORRIDOR +0.70 SIZE – 0.97 PC3	58.51	8.39	3	<0.05
Sttu	-4.31+1.51 SIZE +0.86 PC1 +1.20 PC2	77.20	19.57	3	<0.001
Upep	-2.93+1.31 SIZE –1.87 PC1 – 0.80 PC3	83.51	21.66	3	<0.0001
Pivi	-3.852+0.862 SIZE	70.00	10.57	1	<0.001
Tume	-0.22-0.37 CORRIDOR +1.33 SIZE	78.32	21.49	2	<0.0001
Trtr	-4.40+1.88 SIZE + 1.75 PC1	87.41	32.24	2	<0.0001
Erru	-8.83- 1.28 CORRIDOR +5.33 SIZE +8.21 PC1	100	48.66	2	<0.0001
Lume	-8.17 + 1.12 CONTINUOUS + 2.8 SIZE +5.66 PC1 + 1.5 PC2	85.00	35.92	4	<0.0001
Syme	3.94-2.41 PC3	63.56	9.33	1	<0.01
Syat	2.13-0.93 CONTINUOUS +2.10 PC1 + 2.49 PC2	80.57	18.96	3	<0.001
Phbo	-3.24 +0.99 SIZE	66.12	12.62	1	<0.001
Reig	-8.44 –1.32 CORRIDOR+ 5.31 SIZE + 5.92 PC1	95.50	45.33	3	<0.0001
Aeca	-9.57+5.37 SIZE + 1.71 PC1	90.50	39.65	2	<0.0001
Pama	1.61-3.20 SIZE –1.15 PC2	76.33	20.19	2	<0.0001
Paca	-0.32-0.43 CONTINOUS +1.53 PC2	62.54	7.69	2	<0.05
Pacr	-0.24- 0.35 CORRIDOR +0.75 SIZE	74.23	16.58	2	<0.001
Cebr	-2.84 +2.28 SIZE + 1.12 PC2	85.62	24.56	2	<0.0001
Oror	-4.89+0.92 SIZE	83.33	10.34	1	<0.01
Pipi	2.86-1.31 PC3	50.00	4.23	1	<0.05
Gagl	1.79 – 0.93 CORRIDOR –1.14 CONTINOUS +4.28 SIZE-7.96 PC1	93.50	34.6	2	<0.0001
Pado	3.04-0.94SIZE-1.25 PC3	66.84	12.59	2	0.001
Sese *					
Cach	-1.35+2.03 SIZE +0.60 PC3	71.63	18.58	2	<0.001
Caca	3.46+3.26 PC1	58.92	7.16	1	<0.01
Emci	1.44-0.28CONTINOUS	49.57	2.92	1	<0.1

*No model containing any of the independent variables was included.

Regional density was significantly associated with species occurrence in the Penedes area (r^2=0.25, $F_{1,34}$=10.44, p<0.01). The association was much stronger when forest species were analysed separately from ubiquitous species, in which the association was not significant (r^2=0.25, $F_{1,8}$=2.68, N.S.). Common forest species at a regional scale tend to occupy a larger proportion of fragments than rarer ones (r^2=0.41, $F_{1,24}$=16.67, p<0.001).

DISCUSSION

Most of the forest species, but not ubiquitous species, analysed in the present study (>80%) were influenced by the spatial arrangement of forest fragments, basically size (that accounted for almost 70 % of the total variation in forest species presence), but also by distance to corridors and to large continuous forest habitats. Size is a main determinant of the bird species presence in forest fragments in temperate and boreal habitats (Cieslak 1985, Haila *et al.* 1993, Hinsley *et al.* 1995). Mediterranean forest ecosystems seem to fit the overall pattern and the results of our study were very similar to these obtained by Diaz et al. (1998), who found that fragment size also accounted for about 70 % of the variation in forest bird species of pine forest plantations in the Spanish plateaux. Decreases in forest area decrease the number of species in the remnant fragments, mainly because of the loss of habitat (ex. random sample hypothesis, Connor & McCoy 1979), but also because of the indirect effects of fragmentation on the spatial arrangement of remnant forest patches, such as increased isolation or an increase in edge area (Van Dorp & Opdam 1987, Opdam 1991, Saunders *et al.* 1991, Forman 1995). Indeed, in the Penedes area, distance to corridors significantly affected forest bird presence in fragments, which suggests that the indirect effects of fragmentation such as isolation are also involved in the determination of patterns of species loss in the Mediterranean forests analysed. The fact that distance to continuous forest habitats was also included in some of the specific models of species presence further supports that, at least for some species, isolation partly determines their ability to occupy patches in fragmented Aleppo pine forests. However, the exact effect of stochastic processes on species loss and to which extent this is affected by isolation in Mediterranean forests remains unknown (but see Tellería & Santos 1999). Future studies on the independent assessment of stochastic processes from isolation in species loss are required in order to predict the exact role of fragmentation in bird distribution (Opdam 1991).

The role of other indirect effects of fragmentation on species loss can not be ruled out completely but is difficult to quantify in the present study. In particular, in fragmented forest in North America, increased nest predation near forest edges seems to be an important factor behind decreased habitat quality (Wilcove 1985, Donovan *et al.* 1995, Robinson *et al.* 1995). But similar studies in Mediterranean habitats do not unambiguously support this negative effects and even found that nest predation is higher in forest interior compared to edge habitats (Santos & Tellería 1992). Therefore, the role of indirect edge effects (Murcia 1995), such as nest predation, in Mediterranean fragmented forests remains obscure and waiting for studies that assess simultaneously and identify their relative influence on bird communities.

Forest fragments smaller that 2 ha contained up to around 30 % of the forest species included in our study (Table 5). This contrasts with the 6-10% found by Díaz et al. (1998) in central Spain pine plantations, although the percentage of species in larger fragments was similar in the two studies. Differences in the predominating agricultural matrix may favour the occupancy of smaller fragments by forest species in the Penedes area (Jokimäki & Huhta 1996). Vineyards occupy most of the agricultural areas in the Penedes, whereas cereals form the largest percentage of crops in the Spanish plateaux. As vineyards have a shrubby structure they might facilitate movements of forest species and smooth the loss of species in very small forest fragments. Hinsley *et al.* (1996) also found this rapid increase in species occurrence in Southeast England forest fragments up to about 2 ha. In spite of the geographic distance, there are landscape similarities between Southeast England and the Penedes area. In both cases, the arable and cultivated land is surrounded by hedgerows and riparian vegetation in contrast with the fragments of the Iberian plateaux studied by Díaz *et al.* (1998), which were surrounded of arable land and lacked any shrub or semiarboreal vegetation. Hedgerows and riparian vegetation may enhance the connectivity of the matrix area around forest patches, thus increasing the occurrence of forest species in small patches. Alternatively, the differences in the number of forest species of small patches found between the Penedes area and the Spanish plateaux could be due to the fact that the former is closer to the central European forest ecosystems (due to the proximity of Catalan mountain ranges). In this area, regional density might affect species occurrences and enhance the presence of species in the smallest fragments included in the study (Tellería & Santos 1999). The concordance found between regional abundance for each species and the proportion of fragments it occupies suggests that specific regional abundance is involved in the patterns of species occurrence in our fragmented landscape.

The structure of vegetation also affected species presence significantly. The forest species seem to be positively related, first to subarboreal Mediterranean vegetation such as Holm and Spanish oaks, and second to mature tree cover mainly dominated tall pines. A lower shrub vegetation stratum such as Lentisk and Kermes oak was more associated with the presence/absence of more ubiquitous species. In fact, pine cover up to 8 m did not greatly influence species presence, and if any, pine cover of such height was inversely related to the presence of species such as the Blackcap (*Turdus merula)*, the Blue tit (*Parus caeruleus*) and the Treecreper (*Certhia brachydactyla)*. When PC2, which was related to the cover of pines, was included in the overall model of forest species richness, the results indicated that overall bird presence was indeed favoured by a reduction of overall pine cover and an increase of cover of larger pines (>8 m). These results greatly agree with the only study on the influence of the vegetation structure of Aleppo pine forests on forest birds distributions by López & Moro (1997). The latter concluded that the bird communities studied, located at forest sites in the south-eastern coast of the Iberian peninsula, were better explained by understory characteristics, mainly the presence of Holm oak, than by tree layer variables. A reduction in pine density seemed to have little effect on these bird communities, provided an appropriate understory was conserved. Therefore, the data obtained so far on Aleppo pine forests seem to indicate that bird diversity is favoured by an increase in the number of vegetation layers (MacArthur & MacArthur 1961), namely a rich Holm oak understory and a tree layer with large pines (López & Moro 1997). Furthermore, the long history and extent of shrub habitats in Mediterranean areas (Blondel & Aronson 1999) may have favoured forest bird diversity based on forest habitats containing shrubby and subarboreal features. In addition to the fragment size, forest generalists, which use subarboreal rather than tree vegetation, were more influenced by vegetation structure than by isolation variables such as distance to corridors. On the other hand, forest specialists, which largely depend on a developed tree layer, were more influenced by forest isolation than by tree layer configuration. This suggests that in Mediterranean systems, forest specialists relying on the exploitation of the tree layer are more likely to suffer from the isolation effects associated with fragmentation than forest birds exploiting shrubby and subarboreal vegetation (Tellería & Santos 1995).

In conclusion, breeding bird assemblages in secondary pine forest fragments in the Penedes area were both affected by the spatial arrangement and the vegetation structure of the habitat patches. Our analyses showed that actions aimed to enhance forest bird diversity in such areas would favour larger forests, as fragments of up to 25 ha only contained 50 % of the overall regional diversity in forest bird assemblages (Table 7) . On the other hand, parallel to the increase in the forest habitat, the presence of wooded corridors among forest patches (Table 7) and the distance to continuous forest habitats, together with the restoration of shrubby and subarboreal vegetation, will favour the presence of forest birds in Aleppo pine forest fragments. Main fragmentation effects on forest bird assemblages did not differ greatly from those found in other parts of Europe (Van Dorp & Opdam 1987, Haila *et al.* 1993, Hinsley et al. 1995). As bird communities in Mediterranean and central European forests are surprisingly similar (Blondel & Farré 1988), it is reasonable to expect similar patterns in the species occurrence in fragmented forested landscapes. Therefore, in spite of the large history of human impact, forest birds in Mediterranean mosaics are sensitive to fragmentation and isolation of remnant patches. Future studies should focus on the species regional differences in order to determine which historical factors significantly affect sensitivity to forest fragmentation.

Table 7. Number of forest species predicted to be present in hypothetic forest fragments of variable size and different distances to riparian corridors. The predicted number of forest species present was calculated using a multiple regression model (6.73 – 0.52 log Corridor + 2.15 log Size) on the transformed variables and rounded to the nearest integer.

	DISTANCE TO CORRIDOR		
FRAGMENT SIZE	0 m	100 m	1000 m
1 ha	7	6	6
10 ha	9	8	7
100 ha	11	10	9

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MAIN RESULTS AND DISCUSSION

Post-fire bird succession in dry Mediterranean shrublands

Within the Mediterranean context, the thermo-Mediterranean life-zone is characterised by a warm and dry climate (Blondel & Aronson 1999). Given that the successional dynamics of plants in Mediterranean ecosystems are limited by water availability (Zabala et al. 2000), I hypothesised that the succession of bird communities is very slow in this zone.
The first chapter of this thesis shows that post-fire avian succession in this environment was characterised by a fast recovery of bird abundance and richness. In the third breeding season after fire, avian populations reached the values registered in an unburnt control area; moreover, in the sixth year after fire, controls values were surpassed. These observations were consistent with others in more humid Mediterranean shrublands (Prodon et al. 1984), consequently the initial hypothesis of a slow recovery for these parameters was rejected. However, the rapid recovery of richness and abundance was not followed by a change from communities dominated by open-space species to those dominated by shrubland species, since both groups increased simultaneously during the first six years after the fire. The increase in the number of shrubland species is easily explained by the progressive growth of shrubs. Nevertheless, the abundance of open-space species also increased steadily while vegetation recovered. This can be explained by colonisation of the burnt shrubland from the surroundings, in which open-space species were probably quite scarce due to the lack of large recently burnt extensions. Thus, just after fire, these species moved into the 5000-ha burnt zone and, in spite of the amount of suitable habitat, they did not become abundant. Later, new waves of migrations and local reproduction may have steadily contributed to increasing their abundance. More studies are clearly necessary to confirm this scenario. However, the observation that open-space species remained for so long indicates the suitability of burnt dry Mediterranean habitats for the maintenance of such species, many of which are considered to be in a vulnerable status of conservation in Europe (Tucker & Heath 1994).

Post-fire bird successions are closely linked to vegetation recovery in burnt areas (Prodon et al. 1987, Pons & Prodon 1996). However, in addition to changes in habitat, factors unrelated to the disturbance may also influence the local dynamics of bird populations (Wiens 1989). This thesis shows that the post-fire recovery of habitat cannot be generalised as the only cause of the temporal patterns observed in burnt areas. This is exemplified by observations that the abundance of the Dartford Warbler (*Sylvia undata*) and the Sardinian Warbler (*Sylvia melanocephala*) showed markedly distinct temporal patterns. The increase in the Dartford Warbler population in the burnt area was unrelated to the temporal trend in the unburnt control area, suggesting that habitat changes related to vegetation recovery were associated with its dynamics in the burnt zone. In contrast, the variation in Sardinian Warbler numbers in the burnt zone was parallel to that in the control area, suggesting that processes other than fire were profoundly involved in its post-fire dynamics. These results highlight that bird community succession is constituted by distinct specific responses to a variable number of environmental factors that go further than changes in disturbed habitats.

Fire and the spatial and seasonal variations of bird communities

Species richness is one of the most widely used parameters to analyse the response of communities to habitat alterations, since mature systems are believed to contain more species than disturbed ones (Odum 1961). In burnt dry Mediterranean shrublands, the number of bird species detected in a point-census station was quite low during the first breeding season after fire. Nevertheless, as explained above, richness increased rapidly and the third year after fire this parameter did not differ significantly from that of the unburnt control shrubland. Later, six years after fire, the number of species in the burnt shrubland surpassed the values found in the unburnt one. Therefore, on this small scale (approximately 12 ha), fire could be considered as initially harmful to bird richness but positive at intermediate stages of succession. In France, Prodon et al. (1984) also reported higher bird richness in burnt shrublands than in unburnt controls and suggested that this indicates a higher structural heterogeneity in these successional stages than in previous ones or in controls. Nevertheless, the results of this thesis show that patterns of bird richness greatly depend on the spatial scale considered and, after surveying birds in the whole study zones with 30 point-counts each one, the unburnt shrublands contained more species than those burnt 3 years before.

The scale-effect was also of great relevance when comparing the patterns of bird richness between Aleppo pine forests and dry burnt shrublands. There were more bird species in the stations located in the former than in the latter. However, the species composition of bird communities was less variable among forest stations than among the shrubland stations and, consequently, at a larger scale of observation than single station, burnt shrublands contained almost as many species as forested areas. These results are consistent with those of Forman & Gordon (1986) for many landscapes around the world, in that they reflect that the spatial heterogeneity of these Mediterranean landscapes is scale dependent, which has important repercussions in the spatial structure of bird assemblages.

Habitat structure was much more variable among stations in forested than in burnt areas. Given that habitat structure is one of the main factors that determines the occurrence bird species (McArthur & McArthur 1961, Wiens 1989), this structural pattern was apparently contrasted with that of birds, since the bird communities in burnt zones were more spatially heterogeneous than those of unburnt zones. This pattern was strongly associated with the distinct responses of bird species to variations in habitat structure. Thus, open space species responded to small changes in habitat structure with large changes in their abundance, whereas the response of forest species to these structural variations was significantly lower.

Burnt zones have been reported as areas of interest from the point of view of biodiversity conservation (Blondel & Aronson 1999). About 50% of the bird species found as breeders in burnt zones have a high conservation priority with respect to the particular importance of habitat for their survival (Rocamora 1997). The results of this thesis suggest that habitat management can clearly contribute to improving the populations of open-space bird species since small reductions in the vegetation cover of shrublands affected by fires would lead to an increase in their numbers. Therefore, the maintenance of open areas with low amounts of vegetation, which is of interest to prevent the rapid spread of large wildfires, can also contribute to the conservation of bird diversity. Prescribed fires are increasingly used to help prevent large and catastrophic fires (Miller & Urban 2000). In the Mediterranean shrublands of southern France, Pons (1998) found that these small and incomplete burns increased bird diversity by maintaining previous shrubland species and by allowing the settlement of open-space species. The reintroduction of large herbivores or livestock could also be used to limit vegetation growth in specific zones within the burnt areas.

Given the double interest in diminishing vegetation biomass to prevent large wildfires and in preserving the bird species that inhabit open spaces, it is crucial to carefully select the appropriate zones to act on. If the choice is inappropriate, rapid vegetation recovery may render both objectives unattainable. Therefore, it is recommended to concentrate management actions (prescribed burning, grazing or any other management technique suitable to remove vegetation mass) on specific burnt zones that have slow vegetation growth in order to minimise biomass accumulation, maintain more active fire barriers, and preserve the bird community of open spaces.

The study of the temporal patterns related with fire has focussed on successional changes. Nevertheless, few studies have been devoted to the effects of fire on seasonal changes in bird communities. As mature systems are believed to contain more stable communities than recently disturbed habitats (Odum 1969), I hypothesised that the bird communities in burnt zones undergo greater seasonal shifts than those in forested areas not affected by fire.

Chapter 5 of this thesis shows that, during the wintering season, the zones affected by fire increased the number of forest species, whereas forest sites did not incorporate open-space species. The finding that the range of habitats occupied by species is less restricted in the wintering than in the breeding season is not new (Alatalo 1981, Rice *et al.* 1983, Bilke 1984), but it is interesting to remark that these niche shifts were not the same for all ecological categories and were observed from forest to open habitats but not vice versa.

As expected, from the breeding to the wintering seasons, there was a significant change from communities characterised by summer birds to those characterised by winter birds. This was found in all study zones, independently of the occurrence of fire. Nevertheless, this seasonal shift was more marked in the most recently burnt zone. This finding may be related with the ecological significance of migrations, which are essentially a strategy to adapt to fluctuations in food supply (Stocker & Weihs 1998). Herrera (1978) proposed that high sendentariness in bird populations of Iberian holm-oak forests could be the result of high predictability in the food supply throughout the year. However, Mönkkönen & Helle (1989) showed that the higher predictability of resources in forests was not sufficient to explain residency patterns, since North-American forest bird communities were dominated by migrant species, whereas those in Europe were dominated by all-year resident species. These authors pointed out the role of landscape in wintering grounds, since the proportion of forests is much lower in Africa than in Central and South-America. Therefore, resource predictability in the Mediterranean forests of the Western Palearctic and the scarcity of this type of habitat in African wintering grounds may be related to the high sedentariness of the bird communities that inhabit forests compared with those in recently burnt areas.

In the Aleppo pine forests, bird abundance was significantly higher in the wintering than in the breeding season. Furthermore, in these forests, the difference between the bird abundance of both seasons was similar in two consecutive annual cycles. This contrasts with the total absence of repeatability in burnt ones, where only the second wintering season was characterised by a marked increase in abundance. This pattern suggests a higher annual cyclicity in resource availability in unburnt areas than in those affected by fire. Probably, the abundance of fleshy-fruits, which are a basic food resource for many birds during the wintering season in the Mediterranean (Blondel & Aronson 1999), are subjected to larger interannual variations in burnt areas than in undisturbed ones.

Fire and body condition in birds

The most common approach to the study of the effects of fire on bird species is based on the estimate of species abundance. However, such estimates do not provide direct information about the quality of individuals in distinct habitats (Van Horne 1983), which can be better obtained using individual measures of body condition (Clarke 1992). I studied the body condition of a generalist species that can adapt to most of the post-fire successional stages: the Sardinian Warbler (*Sylvia melanocephala)*. Within the possible measures of body condition, I focussed on the comparison of the fluctuating asymmetry of tail feathers of individuals captured in two dry shrubby zones, one burnt in both 1982 and 1994 and the other burnt only in 1982. Although no conclusive data was found for adults or juveniles with moulted feathers, juveniles with unmoulted rectrices showed higher levels of asymmetry in the zone burnt in 1994. Furthermore, there was a significant association between feather asymmetry and shrub development, which suggests that the differences detected between zones are due to the relationship between habitat quality and vegetation development. These results are consistent with the idea that recently burnt areas are of lower quality for the species. This may be because in low shrublands the competition with Dartford Warblers could force Sardinian Warblers to extend their territories to find tall shrubs for foraging, which could imply a higher energetic cost and higher predation rate (Cody & Walter 1976).

Møller and Swaddle (1997) reported that enhanced asymmetry decreases bird fitness, which may in turn decrease their competitive ability to occupy better quality habitats. Therefore, the results of this thesis indicate that the settlement of juvenile Sardinian Warblers may be affected by their physical condition and that individuals with poor competitive ability may be forced to settle in poorer quality habitats. Therefore, independently of the habitat of origin of juveniles, those that have had a worst development during the initial stages of their lives (and hence have higher asymmetry in the feathers grown when nestlings) could be forced to settle in the recently burnt zone.

Effects of forest fragmentation on birds in Mediterranean landscapes

Several studies have shown that forest fragmentation has deleterious consequences for forest birds. These studies have been basically carried out in landscapes directly modified by human activities such as farming (e.g. Bellamy et al. 1996, Díaz et al. 1998), timber exploitation (e.g. Jokimäki & Hutha 1996, Schmiegelow 1997) or urbanisation (e.g. Mancke & Gavin 2000). However, data on forests fragmented by natural disturbances, such as fire, are scarce. Due to the role of fires in Mediterranean landscapes, I hypothesised a moderate negative effect of this type of fragmentation on forest birds inhabiting fragments of Aleppo pine in the Northeast of the Iberian Peninsula.

As previously reported in continuous Aleppo pine woodlands (López & Moro 1997), local habitat features affected forest bird richness in fragmented forest. Specifically, tree height was positively related to forest canopy species and shrub development with forest understorey species. Once the effect of local habitat features was controlled by using residual analysis, forest bird species were affected by spatial fragment characteristics, which accounted for 29.1% of total variation in forest canopy species and 12.1% in forest understorey species. With regards to the composition and configuration of the landscape surrounding forest patches, only the cover of tall shrublands positively affected canopy species (6.3% of total variance). These results indicate that models of forest bird richness based solely on local habitat features can be misleading in fragmented landscapes.

A significant role of fragment size on forest species was detected, the larger fragments being those that maintained richer forest bird communities. Therefore, as observed in landscapes with other fragmentation histories, forest size is also a determining factor for bird assemblages in fragments of Aleppo pine forest surrounded by a burnt matrix. Nevertheless, the number of forest species detected depended not only on the size of remaining habitat but also on patch configuration. This indicates that bird assemblages were not a random sample of communities from continuous forest tracks (random sample hypothesis, Connor and McCoy 1979) but that they depended on the spatial structure of fragments.

The present study did not show any effect of patch isolation or woodland cover on the number of species, which suggests that, at least for forest birds, the shrubby matrix mitigates the isolation of forest fragments. Forest species richness was highly and positively determined by irregular forest shapes (that is to say, high perimeter/size rates). This result supports the idea of a positive effect of fire-induced fragmentation on Mediterranean forest birds, which contrasts with the common belief that edges are deleterious for most animals that inhabit the interior of the forest fragments (Murcia 1995). The positive effect of edges may be related to other factors that are less frequently reported, such as low nest predation rates (Santos & Tellería 1992), high food availability (Jokimäki et al. 1998) or enhanced opportunities as a result of the new microenvironments created in the amoeboid boundary between the forest and the surrounding shrubland (Forman 1995). Therefore, although edges are often considered negative for forest birds, these results allow the rejection of such generalisations and indicate that the spatial management of forest patches, traditionally based on minimising perimeter/area rate, should be reviewed for Mediterranean landscapes affected by fires.

The effect of forest edges was greater on canopy than on understorey species. For the latter, the shrubby matrix does not differ greatly from their preferred habitat type and therefore, they may perceive a landscape in a much less fragmented way than canopy species do.

In summary, the results of this study indicate that mosaic-like landscapes shaped by fires in the Mediterranean basin do not have a negative impact on forest birds other than that of habitat loss in itself. Historically, Mediterranean forests have been so greatly affected by fragmentation that forest interior bird species are now very scarce or extinct (Tellería 1999). Remaining species have probably adapted to the frequent passage of fire through these woodlands and even exhibit positive associations with the resultant landscape characteristics.

Mediterranean environments have been affected by human activity for many centuries and the process of farmland expansion has led to an intense degradation and fragmentation of forests (Blondel & Aronson 1999). However, to date, no study has focussed on the effects of such fragmentation on bird communities inhabiting in the Aleppo pine forest patches, which are very common in the many areas of the Mediterranean Basin

The last chapter of this thesis shows the importance of habitat loss for bird communities in these Aleppo pine forests. In the Penedès plain, fragment size accounted for around 70% of variation in forest bird richness. Moreover, forest size was also the main predictor of the occurrence of individual forest species, 84% being positively correlated with this variable. As a result of the importance of size, fragments of up to 2 ha contained around 30% of the total number of species in the zone, and those of 25 ha contained around 60%. These percentages were higher in the Penedès than in patches of pine surrounded by cereal croplands in the Iberian plateaux (Díaz et al. 1998), probably because of the differences in matrix permeability, which may greatly affect fragment occupancy patterns (Jokimäki & Huhta 1996). In this case study, the shrubby matrix constituted by vineyards might facilitate movements of forest birds and hence smooth the loss of species in fragments. Furthermore, differences between areas could be also related to regional variations in bird density, which significantly influenced species in both the study zone and the Iberian Plateaux (Tellería & Santos 1999).

Distance to continuous woodlands or to riparian-forested corridors was significant for the occurrence of 47% of forest species, which shows that isolation partly determines their ability to occupy fragments. Nevertheless, the relative importance of isolation differed between forest specialists and forest generalists. The richness of the former, which basically inhabit tree canopies, was more affected by distance to corridors, whereas forest generalists, which use subarboreal rather than tree layers, were more influenced by vegetation structure. This data suggests that in these Mediterranean agricultural landscapes, forest specialists are more likely to suffer from the effects of fragment isolation associated with fragmentation than forest generalists.

MAIN CONCLUSIONS

1. In dry thermo-Mediterranean shrublands, avian succession induced by fires is very fast with respect to the recovery of bird richness and abundance. However, the change from communities dominated by open-space species to those dominated by shrubland species is much slower, since both groups increase in parallel during the first years after fire, which reflects the maintenance of a heterogeneous mosaic of open and shrubby zones. In contrast with shrubland fires, available data strongly suggests that fires in dry Aleppo pine forests entail a very slow recovery (several decades) of forest bird communities.
2. It is generally accepted that the drastic habitat modification involved in successions determines changes in bird species abundance. Nevertheless, the data obtained in this thesis indicates that the post-fire dynamics in burnt areas can sometimes be linked to external population trends that are unrelated to the occurrence of fire. This is exemplified by the Sardinian Warblers that inhabited a shrubland area burnt in 1994. The population trend of this species was closely associated with that of the neighbouring unburnt area. In contrast, the trend of the Dartford Warbler population in the burnt zone was totally unrelated to that of the unburnt area and therefore can be essentially attributed to post-fire habitat changes. This result highlights that bird community succession after fire involves the responses of different species to a variable number of environmental factors that go beyond local habitat changes.
3. Patterns of bird richness depend on the spatial scale considered. Although unburnt forests contain high bird richness on a small scale, the avian communities of these areas are spatially highly uniform. In contrast, burnt areas have low bird richness on a small spatial scale but the large spatial heterogeneity of these communities allows an increase in richness when increasing the scale considered.
4. Forest species are very resilient to changes in forest structure, whereas open-space species are highly sensitive to small variations in habitat structure. This is of interest from a conservation point of view since habitat management can be a suitable tool for managing bird populations in burnt areas, where more than 50% of species are considered to be either decreasing or in a vulnerable situation.
5. Burnt areas undergo higher seasonal variation in bird assemblages than those unaffected by fire. Furthermore, seasonal oscillations in bird abundance seem more repeatable year after year in unburnt areas, probably as a result of higher annual ciclicity in resource availability.
6. The Sardinian Warbler is a highly generalist Mediterranean species that can adapt to habitats as diverse as burnt areas to dense forests. However, habitat type affects the quality of the individuals. The body condition that juveniles have when finished their development determines their posterior settlement, in such a way that low quality individuals settle in burnt areas, where the shrub layers are poorly developed.
7. Apart from the loss of available habitat, fire-induced fragmentation of Aleppo pine forests has a low impact on forest birds. Neither the isolation of remnant forest patches nor woodland cover in the surrounding landscape affect forest bird richness, suggesting that the shrubland matrix is highly permeable for these species. Indeed, the increased perimeter/size rate of remaining forests enhance the richness of forest birds, indicating that the boundaries between shrublands and forests are perceived as advantageous microhabitats. Hence, the concept of ideal patch, traditionally based on the minimisation of the perimeter/size rate, should be reviewed, at least for landscapes affected by fires.

8. Forest fragment size is the main factor involved in forest bird richness in agricultural areas and fragments must be quite large to support a rich bird community. In the Penedès plain, forests of up to 2 ha contain 30% of the regional species pool and even fragments of 25 ha have only around 60%. Furthermore, the bird assemblages of these forest fragments do not correspond to random samples of continuous tracts of forests but are shaped by their spatial configuration. Thus, in contrast with forest bird assemblages residing in Aleppo pine patches resulting from fire, those located in an agricultural matrix can be affected by fragment isolation. Special attention should be paid to riparian forested corridors that cross farmlands as they contribute to increasing bird richness in nearby forest patches.
9. In landscapes containing fragmented forests, such as those originated in fire dynamics or farming, the composition of forest bird communities is not only affected by local habitat features but by the spatial configuration of the forest patches. Nevertheless, not all species respond similarly and forest canopy species can be more affected by patch configuration than understorey species.
10. Although birds that breed in Aleppo pine forests are quite resilient to alterations in habitat structure, appropriate forest management even can favour them. Forest canopy species are positively related to the tree height, which can be enhanced by a reduction in tree density through selective cutting. However, management practices should avoid the elimination of shrubby vegetation, which is essential for understorey species.

RESULTATS PRINCIPALS I DISCUSSIÓ

La successió ornítica després del foc en màquies mediterrànies

Dins del context mediterrani, la zona termo-mediterrània es caracteritza per una climatologia càlida i seca (Blondel & Aronson 1999). Donat que la dinàmica successional de les plantes en sistemes mediterranis està limitada per la disponibilitat d'aigua (Zabala et al. 2000), vaig hipotetitzar que la successió de la comunitat d'ocells seria molt lenta en aquest ambient.

El primer capítol d'aquesta tesi mostra la successió post-incendi en aquest medi, que es va caracteritzar per una ràpida recuperació de l'abundància i riquesa d'ocells. Es van assolir els valors dels controls no cremats durant la tercera temporada de nidificació després del foc i fins i tot van ser sobrepassats el sisè any després de l'incendi. Aquest resultat rebutja la hipòtesi inicial de la lenta recuperació d'aquests paràmetres i mostra una rapidesa comparable a la trobada en altres comunitats arbustives mediterrànies més humides (Prodon et al. 1984). No obstant, la ràpida recuperació de la riquesa i l'abundància no va ser seguida per un canvi des de comunitats dominades per espècies d'espais oberts cap a comunitats dominades per espècies d'ambients arbustius, ja que tots dos grups van augmentar simultàniament durant els primers sis anys després del foc. L'increment en el número d'espècies d'ambients arbustius s'explica amb facilitat pel progressiu creixement dels arbustos. Però tanmateix, l'abundància d'espècies d'espais oberts també va augmentar progressivament a mida que la vegetació es recuperava. Això podria estar relacionat amb el procés de colonització de la màquia cremada des dels voltants, on probablement les espècies d'espais oberts eren prou escasses degut a la manca de grans extensions recentment cremades. Per aquest raó, just després del foc, les espècies aquestes espècies van haver d'escampar-se en una zona cremada de 5000 ha i llavors, tot i la gran quantitat d'hàbitat adequat, no van poder resultar abundants. Posteriorment, noves onades d'immigrants i la reproducció local podrien contribuir progressivament a l'augment en la seva abundància. Òbviament, calen més estudis per confirmar o no aquest escenari. Però, en qualsevol cas, el cas que les espècies d'espais oberts es mantinguin tant temps indica la idoneïtat dels hàbitats mediterranis eixuts i cremats per al manteniment d'aquestes espècies, moltes de les quals es consideren en estat de conservació vulnerable a Europa (Tucker & Heath 1994).

Les successions post-foc dels ocells estan estretament lligades a la recuperació de la cobertura vegetal de les àrees cremades (Prodon et al. 1987, Pons & Prodon 1996). Tot i això, a més dels canvis en els hàbitats, factors no relacionats amb la pertorbació poden influir en la dinàmica de les poblacions d'ocells (Wiens 1989). Aquest tesi evidencia que la recuperació de l'hàbitat després del foc no pot ser generalitzada com la única causa que hi ha al darrera dels patrons temporals observats a les àrees cremades. En aquest sentit, les abundàncies de tallareta cuallatga (*Sylvia undata*) i tallarol capnegre (*Sylvia melanocephala*) mostren un patró temporal marcadament diferent que serveix per exemplificar-ho. L'augment de les poblacions de tallareta cuallarga a les zones cremades no va estar correlacionada amb les tendències temporals que van ocórrer a la zona no cremada control, suggerint que els canvis en l'hàbitat relacionats amb la recuperació vegetal estaven al darrera de la seva dinàmica a la zona cremada. Però, en contrast, la variació en el nombre de tallarols capnegres a la zona cremada va ser paral·lel a la ocorreguda a la zona control, suggerint que processos diferents del foc estaven profundament involucrats en la seva dinàmica post-foc. Aquests resultats remarquen que la successió de la comunitat d'ocells està constituïda per un conjunt de diferents respostes específiques a un nombre variable de factors ambientals que van més enllà dels canvis en els hàbitats pertorbats.

El foc i les variacions espacials i estacionals de les comunitats d’ocells

La riquesa d’espècies és un dels paràmetres més àmpliament utilitzats per analitzar la resposta de les comunitats a les alteracions dels hàbitats, ja que es considera que els sistemes madurs contenen més espècies que els pertorbats (Odum 1961). A les màquies cremades, el nombre d’espècies d’ocells detectades en una estació de cens puntual va ser bastant baix durant la primera estació de nidificació després del foc. Amb tot, tal i com s’ha explicat anteriorment, la riquesa va augmentar ràpidament i aquest paràmetre no va diferir significativament dels de la màquia control no cremada.

Més endavant, als sis anys després del foc, el nombre d’espècies va sobrepassar els valors de la màquia control. Per tant, per aquesta petita escala (aproximadament 12 ha), el foc podria ser considerat com inicialment nociu per a la riquesa d’ocells, però positiu en estadis successionals intermedis. A França, Prodon et al. (1984) també van trobar una major riquesa d’ocells en les comunitats arbustives cremades que en controls no cremats i, tal i com suggerien aquests autors, aquest fet sembla indicar una més alta heterogeneïtat estructural en aquests estadis successionals que en els anteriors o que en els controls. Amb tot, els resultats d’aquesta tesi mostren que els patrons de riquesa d’ocells depenen altament de l’escala espacial considerada i, després de mostrejar ocells en el conjunt de les zones d’estudi amb 30 punts d’escolta cadascuna, la màquia no cremada contenia més espècies que la cremada.

L’efecte de l’escala va tenir també una gran rellevància el comparar els patrons de riquesa ornítica entre les pinedes de pi blanc i les màquies cremades. Hi va haver més espècies d’ocells a les estacions de mostreig forestals que en les de les màquies cremades. No obstant, la composició específica de les comunitats d’ocells va ser menys variable entre les estacions forestals que entre les de les màquies cremades i, com a conseqüència, en una escala d’observació més gran que una estació de mostreig, les màquies cremades van tenir gairebé tantes espècies com es boscos. Tal i com van mostrar Forman & Gordon (1986) per a molts paisatges del món, aquests resultats reflecteixen que la heterogeneïtat espacial d’aquests paisatges mediterranis és depenent de l’escala, la qual cosa té importants repercussions en l’estructura espacial de les comunitats d’ocells.

L’estructura de l’hàbitat va ser molt més variable entre estacions de mostreig a les zones forestals que a les cremades. Considerant que l’estructura de l’hàbitat és un dels principals factors que determinen la presència de les espècies d’ocells (McArthur & McArthur 1961, Wiens 1989), aquest patró estructural va estar en aparent contradicció amb el dels ocells, car les comunitats d’ocells que habitaven les zones cremades van ser molt més espacialment heterogènies que les de zones no cremades. Aquest fet estava fortament associat amb les diferents respostes de les espècies d’ocells a les variacions de l’estructura de l’hàbitat. D’aquesta manera, les espècies d’espais oberts responien a petits canvis en l’estructura de l’hàbitat amb grans canvis en la seva abundància, mentre que la resposta de les espècies forestals a aquestes variacions estructurals era significativament menor.

Les zones cremades han estat citades com àrees interessants des del punt de vista de la conservació de la biodiversitat (Blondel & Aronson 1999). Al voltant d’un 50% de les espècies trobades coma nidificants a les zones cremades tenen una alta prioritat de conservació pel que fa a la importància de l’hàbitat per a la seva supervivència (Rocamora 1997). Els resultats d’aquesta tesi suggereixen que el maneig dels hàbitats poden clarament contribuir a millorar les poblacions de les espècies d’espais oberts ja que petites reduccions en la cobertura vegetal de les màquies afectades pels focs determinaria un increment en els seus efectius. Per tant, les pràctiques portades a terme per a mantenir àrees obertes amb baixes quantitats de matèria vegetal, les quals estan rebent un interès en augment per evitar la violenta progressió dels grans incendis, poden també contribuir a preservar la diversitat d'ocells. Els focs prescrits són cada cop més utilitzats com a una eina de gestió que pot ajudar a prevenir els catastròfics incendis de grans dimensions (Miller & Urban 2000). A les comunitats arbustives del sud de França, Pons (1998) va trobar que aquestes cremes petites i incompletes incrementaven la diversitat d'ocells perquè mantenien les espècies d'ambients arbustius i permetien l'establiment d'espècies d'ambients oberts. La reintroducció dels grans herbívors o de ramats domèstics és una altra possible estratègia que pot ser utilitzada per tal de limitar el creixement de la vegetació en zones específiques dins les àrees cremades.

Donat el doble interès en disminuir la biomassa vegetal per evitar els grans incendis i preservar les espècies d'ocells que viuen en espais oberts, és molt important seleccionar acuradament les zones apropiades on actuar. Si l'elecció es desafortunada, la ràpida recuperació de la vegetació pot fer que inassolibles els dos objectius. Per tant, es recomanable concentrar les accions de gestió (cremes controlades, activitat pastoral o qualsevol altra tècnica apropiada per eliminar massa vegetal) a zones cremades específiques que presentin un lent creixement vegetal de tal forma que l'acumulació de biomassa sigui minimitzada, les barreres contra el foc es mantinguin més actives, i la comunitat d'ocells d'espais oberts preservada.

L'estudi dels patrons temporals relacionats amb el foc s'ha centrat en els canvis successionals. No obstant, hi ha pocs estudis sobre els efectes del foc en els canvis estacionals de les comunitats d'ocells. Com que es considera que els sistemes madurs contenen comunitats més estables que els recentment pertorbats (Odum 1969), vaig hipotetitzar que les comunitats d'ocells de les zones cremades patien majors canvis estacionals que les de zones forestals no afectades pel foc.

El capítol 5 d'aquesta tesi mostra que, durant l'estació d'hivernada, les zones afectades pel foc augmentaven el nombre d'espècies forestals, mentre que els llocs forestals no incorporaven espècies d'espais oberts. Trobar que el rang d'hàbitats ocupat per les espècies és menys restringit a l'estació d'hivernada que a la de nidificació no és nou (Rice *et al.* 1983, Bilke 1984), però és interessant remarcar que aquest canvis de nínxol no van ser iguals per a totes les categories ecològiques i es van evidenciar des dels hàbitats forestals cap als oberts però no en sentit oposat.

Tal i com s'esperava, des de l'estació de nidificació a la d'hivernada, es va detectar un canvi significatiu des de comunitats caracteritzades per ocells propis de l'estiu cap a comunitats caracteritzades per ocells propis de l'hivern. Això es va trobar en totes les zones, independentment de si havia estat cremada o no. Tot i això, aquest canvi estacional va estar més marcat a la zona cremada més recentment. Aquest resultat pot estar relacionat amb la significació ecològica de les migracions, les quals són essencialment una estratègia per adaptar-se a les fluctuacions en la disponibilitat d'aliment (Stocker & Weihs 1998). Herrera (1978) va proposar que l'elevat sedentarisme en les poblacions d'ocells dels alzinars ibèrics podia ser el resultat d'una alta predictabilitat en la disponibilitat d'aliment al llarg del tot l'any. Amb tot, Mönkkönen & Helle (1989) van mostrar que l'alta predictabilitat en els recursos forestals no era suficient per explicar els patrons de residència, ja que les comunitats d'ocells forestals nord-americanes estaven dominades per espècies migradores, mentre que les europees ho estaven per espècies residents al llarg de l'any. Aquests autors apunten el paper que el paisatge pot tenir en els llocs d'hivernada, ja que la proporció de boscos és mol menor a l'Àfrica que a Centre o Sud Amèrica. Per tant, la predictabilitat de recursos als boscos mediterranis del Palearctic Occidental i l'escassetat d'aquests hàbitats als quarters d'hivernada africans podrien estar al darrera de l'alt sedentarisme de les comunitats d'ocells forestals comparades amb les de les àrees recentment cremades.

A les pinedes de pi blanc, l'abundància d'ocells va ser significativament més elevada a l'estació d'hivernada que a la de nidificació. A més, en aquests boscos, la diferència entre l'abundància d'ocells entre ambdues estacions va ser similar en dos cicles anuals consecutius. Això contrasta amb la total absència de repetibilitat a les zones cremades, on només la segona temporada d'hivernada va estar caracteritzada per un marcat increment en l'abundància d'ocells. Aquest patró suggereix una major ciclicitat anual en la disponibilitat de recursos a les zones no cremades que en les afectades pel foc. Probablement l'abundància de fruits, que en el mediterrani són una font bàsica de recursos per a moltes espècies durant la temporada d'hivernada (Blondel & Aronson 1999), estan subjectes a unes majors variacions interanuals a les àrees cremades que a les no pertorbades.

Foc i condició física en ocells

L'aproximació més habitual a l'estudi dels efectes del foc en les espècies d'ocells es basa en l'estima de les abundàncies de les espècies. No obstant, aquestes estimes no proporcionen informació directa sobre la qualitat dels individus en els diferents hàbitats (Van Horne 1983), les quals poden obtenir-se millor utilitzant mesures individuals de la condició física (Clarke 1992). Vaig estudiar la condició física d'una espècie generalista que és capaç de viure en la major part de la sèrie successional després del foc: el tallarol capnegre (*Sylvia melanocephala*). Dintre del nombre de possibles mesures de condició física, em vaig centrar en la comparació de l'asimetria fluctuant de les plomes de la cua dels individus capturats en dues zones de màquia, una cremada dues vegades, l'any 1982 i l'any 1994, i l'altre només l'any 1982. Tot i que no es van trobar dades concloents per a adults i juvenils que havien mudat les plomes de la cua, els juvenils amb rectrius no mudades van mostrar uns majors nivells d'asimetria en la zona cremada l'any 1994. A més, es va trobar una associació significativa entre l'asimetria de les plomes i el desenvolupament arbustiu, la qual cosa suggereix que la diferència detectada entre zones és deguda a les relacions entre la qualitat de l'hàbitat i el desenvolupament de la vegetació. Aquest resultats són consistents amb la idea que els llocs recentment cremats són de més baixa qualitat per l'espècie. Probablement això es degut a que a les comunitats arbustives baixes la competència amb la tallareta cuallarga pot forçar al tallarol capnegre a tenir uns territoris més grans per trobar suficients arbustos alts on menjar, la qual cosa pot implicar majors costos energètics i majors taxes de predació (Cody & Walter 1976).

Møller i Swaddle (1997) van aportar evidències que altes asimetries disminueixen l'eficàcia biològica dels ocells, cosa que pot afectar negativament la seva capacitat competitiva per ocupar els hàbitats de millor qualitat. Així doncs, els resultats d'aquest estudi semblen indicar que l'establiment dels juvenils de tallarol capnegre pot estar influenciat per la seva condició física i que els individus amb una pobre aptitud competitiva poden ser forçats a establir-se en hàbitats amb una qualitat més baixa. Per tant, independentment de l'origen dels juvenils, els que han tingut un pitjor desenvolupament durant les etapes inicials de les seves vides (i per tant presenten uns majors nivells d'asimetria a les plomes que han crescut mentre eren al niu) poden ser forçats a establir-se als llocs recentment cremats.

Efectes de la fragmentació forestal en ocells en paisatges mediterranis

Diversos estudis han mostrat que la fragmentació forestal té conseqüències negatives per als ocells forestals. Amb tot, aquests estudis han estat bàsicament portats a terme en paisatges directament modificats per activitats humanes com l'agricultura (e.g. Bellamy et al. 1996, Díaz et al. 1998), l'explotació forestal (e.g. Jokimäki & Hutha 1996, Schmiegelow 1997) o la urbanització (e.g. Mancke & Gavin 2000), però dades referents a boscos fragmentats per pertorbacions natural com el foc són escasses. Degut al paper dels focs en els paisatges mediterranis, vaig hipotetitzar un efecte negatiu moderat d'aquest tipus de fragmentació sobre els ocells que habitaven fragments de pineda de pi blanc del nord-est de la península Ibèrica.

Tal i com ja ha estat citat per boscos continus de pi blanc (López & Moro 1997), les característiques locals dels hàbitats afecten la riquesa d'ocells forestals en boscos fragmentats. Concretament, l'alçada dels arbres va estar positivament relacionada amb les espècies forestals de capçada i el desenvolupament dels arbustos amb les espècies de sotabosc. Un cop controlat aquest efecte de les característiques locals de l'hàbitat a través de l'anàlisi dels residuals, les espècies forestals van estar afectades per les característiques espacials dels fragments, que van aportar el 29.1% de la variació total en espècies de capçada i el 12.1% en espècies de sotabosc. En relació a la composició i configuració del paisatge del voltant dels fragments forestals, només la cobertura de vegetació arbustiva alta va afectar positivament les espècies de capçada (6.3% de la variació total). Aquests resultats indiquen que els models de riquesa d'espècies forestals únicament basats en les característiques locals dels hàbitats poden ser erronis en paisatges fragmentats.

Es va trobar un paper significatiu de la mida dels fragments en les espècies forestals, essent els fragments més grans els que mantenien comunitats d'ocells forestals més riques. Per tant, tal i com ha estat observat en paisatges amb altres històries de fragmentació, la mida dels fragments és també un factor determinant per a les comunitats d'ocells dels fragments de bosc de pi blanc envoltats per una matriu cremada. Tanmateix, el nombre d'espècies forestals detectades van dependre no només de la mida de l'hàbitat restant sinó també de la configuració dels fragments. Això indica que aquestes comunitats d'ocells no eren mostres aleatòries de comunitats de trams continus de bosc (random sample hypothesis, Connor & McCoy 1979), sinó que depenien de l'estructura espacial dels fragments.

Aquest estudi no mostra cap efecte de l'isolament dels fragments ni de la cobertura forestal del paisatge en el nombre d'espècies, la qual cosa suggereix que, almenys per als ocells forestals, la matriu arbustiva mitiga l'isolament dels fragments forestals. La riquesa d'espècies forestals va estar altament i positivament determinada per formes irregulars en els fragments (és a dir, per alts quocients perímetre/àrea). Aquest resultat recolza la idea d'efectes positius d'aquesta fragmentació lligada als incendis en ocells forestals mediterrànies, la qual cosa contrasta amb la visió general de les vores com negatives per a molts animals propis de l'interior dels fragments (Murcia 1995). Les influències positives de les vores poden estar relacionades amb altres factors menys freqüentment citats, com ara baixes taxes de predació (Santos & Tellería 1992), alta disponibilitat d'aliments (Jokimäki et al. 1998) o millora de les oportunitats com a conseqüència dels nous microambients creats pels contactes ameboids entre els boscos i les zones arbustives del voltant (Forman 1995). Per tant, tot i que sovint les vores s'han considerat negatives pels ocells forestals, aquests resultats permeten rebutjar aquestes generalitzacions i indiquen que la gestió espacial dels fragments forestals, tradicionalment basada en la minimització de les relacions perímetre/àrea, haurien de ser revisades en paisatges Mediterranis afectats pel foc.

Les vores de bosc van influenciar més a les espècies de capçada que a les de sotabosc. Per a les espècies de sotabosc, la matriu arbustiva no difereix molt del seu hàbitat preferit i, per tant, probablement perceben el paisatge d'una manera molt menys fragmentada de com ho fan les espècies de capçada.

En resum, els resultats d'aquest estudi indiquen que els paisatges en mosaic modelats pel foc a la mediterrània no estan associats amb efectes de fragmentació negatius sobre les espècies forestals, amb l'excepció dels relacionats amb la pèrdua d'hàbitat. Els boscos mediterranis han estat històricament tant afectats per la fragmentació que les espècies de l'interior forestal són actualment molt escasses o estan extingides (Tellería 1999). Probablement, les espècies que han persistit s'han adaptat al freqüent pas del foc a través de les zones boscoses i fins i tot exhibeixen associacions positives amb les característiques paisatgístiques creades per aquesta pertorbació.

Els ambients mediterranis han estat afectats per les activitats de l'home durant molts segles i el procés d'expansió de les terres conreades ha comportat una intensa degradació i fragmentació forestal (Blondel & Aronson 1999). Tot i això, fins ara, cap estudi s'ha centrat en els efectes d'aquesta fragmentació en les comunitats d'ocells que habiten els fragments de pinedes de pi blanc, les quals són molt comunes a moltes àrees de la conca mediterrània.

El darrer capítol d'aquesta tesi mostra la importància de la pèrdua d'hàbitat per als ocells que viuen en boscos de pi blanc fragmentats. A la plana del Penedès, la mida del fragment va explicar al voltant d'un 70% de la variació de la riquesa d'espècies d'ocells forestals. A més, la mida dels fragments va ser també el principal predictor de la presència d'espècies forestals, de tal manera que el 84% d'aquestes espècies estaven positivament correlacionades amb aquesta variable. Degut a la importància de la mida, els fragments de fins a 2 ha contenien al voltant d'un 30% del nombre total d'espècies de la zona i fragments de 25 ha en tenien un 60%. Aquests percentatges van ser més elevats al Penedès que a les pinedes fragmentades i envoltades per conreus cerealístics de la Meseta Ibèrica (Díaz et al. 1998), probablement a conseqüència de les diferències en la permeabilitat de la matriu, que pot afectar de manera notable els patrons d'ocupació dels fragments (Jokimäki & Huhta 1996). En el cas estudiat, la matriu arbustiva formada per les vinyes podria facilitar els moviments de les espècies forestals i per tant suavitzar la pèrdua d'espècies en els fragments. A més, aquestes diferències entre àrees poden també estar relacionades amb variacions regionals en la densitat dels ocells, les quals influencien significativament la presència d'espècies tant a la zona estudiada com a la Meseta Ibèrica (Tellería & Santos 1999).

La distància a les zones boscoses contínues o bé als corredors forestals riberencs va ser significativa per a la presència d'un 47% de les espècies forestals, la qual cosa revela que l'isolament determina parcialment la seva capacitat d'ocupar els fragments. Amb tot, la importància relativa de l'isolament va diferir entre les espècies forestals especialistes i les generalistes. La riquesa d'espècies forestals especialistes, les quals són viuen bàsicament a les capçades, va estar més afectada per la distància als corredors, mentre que el nombre d'espècies generalistes, les quals utilitzen més els estrats subarboris més que no pas els arbres, va estar més influenciat per l'estructura de la vegetació. Aquesta dada suggereix que en aquests paisatges agrícoles mediterranis és més probable que les espècies forestals especialistes pateixin els efectes de l'isolament associats a la fragmentació que les generalistes.

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CONCLUSIONS PRINCIPALS

11. A les eixutes comunitats arbustives thermo-mediterrànies, la successió ornítica induïda pels incendis és molt ràpida pel que fa a la recuperació de la riquesa i l'abundància d'ocells. No obstant, el canvi des de comunitats dominades per les espècies d'espais oberts a espècies pròpies d'ambients arbustius és molt més lenta, ja que els dos grups d'espècies incrementen en paral·lel durant els primers anys després del foc, la qual cosa reflecteix el manteniment d'un mosaic heterogeni de zones obertes o arbustives. Contrastant amb els incendis sobre zones arbustives, les dades disponibles suggereixen clarament que els focs en pinedes de pi blanc comporten una molt lenta recuperació (vàries dècades) de la comunitat d'ocells forestals.
12. Està generalment acceptat que la dràstica modificació de l'hàbitat implicada en les successions determina els canvis en l'abundància de les espècies. Tanmateix, les dades obtingudes indiquen que la dinàmica post-incendi de les zones cremades de vegades pot estar bàsicament lligada a tendències poblacionals no relacionades amb el pas del foc. Aquest és el cas dels tallarols capnegres que habitaven una màquia cremada al 1994, on la seva tendència poblacional va estar estretament associada amb la de la veïna zona no cremada. Per contra, l'evolució de les poblacions de tallareta cuallarga a la zona cremada va estar absolutament deslligada de la de la zona no cremada i per tant, pot ser atribuïda essencialment als canvis post-incendi en l'hàbitat cremat. Aquests resultats emfatitzen el fet que la successió de la comunitat d'ocells després del foc és un compendi de les diferents respostes de cada espècie a un nombre variable de factors ambientals que van més enllà dels canvis locals en l'hàbitat.
13. Els patrons de riquesa d'ocells depenen molt de l'escala espacial considerada. Tot i que els boscos no afectats pel foc contenen una riquesa d'espècies elevada a petita escala, les comunitats d'ocells d'aquests ambients són molt uniformes en l'espai. En canvi, les àrees cremades tenen una baixa riquesa d'ocells a petita escala però la gran heterogeneïtat espacial d'aquestes comunitats permet un increment de la riquesa quan augmentem l'escala considerada.
14. Les espècies forestals presenten una alta resiliència als canvis en l'estructura del bosc, mentre que les espècies d'espais oberts són molt sensibles a petites variacions en l'estructura de l'hàbitat. Això té unes implicacions interessants des d'un punt de vista de la conservació ja que el maneig de l'hàbitat pot ser una eina apropiada per a la gestió de les poblacions d'ocells de les àrees cremades, on es considera que més del 50% de les espècies estan el regressió o en situació vulnerable.
15. Les comunitats d'ocells de les àrees cremades pateixen unes variacions estacionals majors que les de les zones no afectades pel foc. A més, les oscil·lacions estacionals en l'abundància d'ocells semblen més repetibles any rera any en les zones no cremades, probablement com conseqüència d'una major ciclicitat anual en la disponibilitat de recursos en aquestes zones.
16. El tallarol capnegre és una espècie mediterrània molt generalista que és capaç d'habitar des de les zones cremades fins els boscos densos. Tanmateix, hi ha diferències entre la qualitat dels individus que hi ha en un hàbitat o un altre. La condició física que els juvenils presenten al acabar el seu desenvolupament condiciona el seu establiment posterior, de tal manera que els individus de més baixa qualitat van a parar a les zones recentment cremades, on l'estrat arbustiu hi està poc desenvolupat.
17. Apart de la pèrdua d'hàbitat disponible, la fragmentació dels boscos de pi blanc deguda als incendis provoca un baix impacte en els ocells forestals. Ni l'isolament

dels fragments, ni la cobertura forestal del paisatge del voltants afecten la riquesa d’ocells forestals, la qual cosa suggereix que la matriu arbustiva és altament permeable per a aquestes espècies. A més, les altes relacions perímetre/mida dels fragments influeixen positivament la riquesa d’ocells forestals, indicant que les vores entre les comunitats arbustives i els boscos són percebudes com microhàbitats avantatjosos. Així doncs, el concepte de fragment ideal, tradicionalment basat en la minimització de les relacions vora/mida, hauria de ser revisat, com a mínim, per aquests paisatges afectats pels incendis.

18. La mida dels fragments és el principal factor implicat en la riquesa d’ocells forestals en àrees agrícoles, les quals han de ser bastant grans per a mantenir una rica comunitat d’ocells. A la plana del Penedès, els boscos de fins a 2 ha contenen un 30% del conjunt d’espècies forestals de la regió i mentre que fragments de 25 ha només en contenen aproximadament un 60%. A més, el conjunt d’ocells d’aquests fragments no correspon a una mostra aleatòria de trams continus de bosc sinó que està determinat per la seva configuració espacial. Per tant, i a diferència de les comunitats d’ocells dels fragments de bosc de pi blanc originats pels incendis, els que estan localitzats dins una matriu agrícola poden estar afectats per l’isolament. Menció especial mereixen els corredors riberencs forestals que travessen les àrees conreades, els quals contribueixen a incrementar la riquesa d’ocells dels bosquets propers.
19. En paisatges amb boscos fragmentats, com els originats en la dinàmica del foc o en el conreu de la terra, la composició d’ocells forestals no està només afectada per les característiques locals de l’hàbitat sinó també per la configuració espacial dels boscos-illa. Amb tot, no totes les espècies en responen igual, de tal forma que les espècies de capçada estan molt més afectades per la configuració dels fragments forestals que les de sotabosc.
20. Tot i que els ocells que nidifiquen en boscos de pi blanc són bastant resilients a les alteracions en l’estructura de l’hàbitat, un gestió forestal apropiada els en pot resultar fins i tot positiva. Les espècies forestals de capçada estan positivament relacionades amb el desenvolupament vertical dels arbres, la qual cosa pot ser millorada a través de tales selectives que redueixin la densitat de peus. No obstant, les pràctiques de gestió haurien d’evitar l’eliminació de la vegetació de sotabosc, que és essencial per a les espècies de sotabosc.

ENVOLTANT AQUESTA TESI

Bé, acabo de passar-li al Robin el “Chapter 9” per que se’l miri i, més relaxat, em poso a escriure l’única part de la tesi que em sembla que no cal fer en anglès: els agraïments. Sospiro...haver arribat aquí representa una gran satisfacció.
Hi ha dues persones que han estat realment imprescindibles per a la consecució d’aquesta tesi i per això mateix voldria començar per elles. I és que sense el Santi Llacuna i el Dr. Nadal res no hagués ni començat. Amb el Santi vam dissenyar el projecte de tesi, projecte que, a mida que passava el temps, s’ha anat desenvolupant amb modificacions importants respecte la primera versió, però per al que hem pogut mantenir l’essència inicial. Quatre anys són molts anys, o al menys hi passen moltes coses...Vull destacar el suport que en tot moment he tingut per part del meu director de tesi, que, com a amic que és, ha anat molt més enllà del que hi ha al voltant d’aquesta tesi. L’estiu de 1996 en Santi Llacuna em va presentar el Dr. Nadal, amb qui també he obtingut molt més que un grup investigador on recolzar-me científica i econòmicament (Beca FPI). El Dr. Nadal... qui l’ha conegut sap fins on arriba la seva extraordinària capacitat per posar-se al lloc de l’altre i trobar un camí de sortida als seus problemes. No tinc paraules.

Dins el recorregut per les persones que han contribuït a la realització d’aquesta tesi, el Lluís Brotons hi té un paper cabdal. La seva intervenció en tots els capítols és prou indicativa. El seu suport ha estat molt ampli i ha anat des de l’anàlisi de dades a la redacció dels articles, del plantejament d’hipòtesis a la feina de camp, dels congressos a les migdiades al cotxe. D’una punta l’altre d’aquesta tesi, la seva empremta és patent. Lluís, ha estat (és) un plaer treballar junts. Quedem per sopar a l’Ugarit amb la Laia i l’Olga?

Provinent més aviat d’altres camps de la biologia com ara la fitosociologia i l’ecologia, els meus inicis com a ornitòleg van estar (i encara estan) lligats a la relació que hi ha entre els ocells i el seu ambient. Però hi va haver un pas previ a la realització d’aquest tesi que va ser clau: l’aprofundiment en el món auditiu i visual que són els ocells. És aquí on cal esmentar el paper del Rodrigo del Amo. Gràcies Rodri, per tot el que hem compartit.

Aquesta ha estat una tesi amb força treball camp. Els qui n’heu fet sabreu que és potser la part de la feina que proporciona les experiències més polaritzades: hi ha dies que poden ser una absolut fracàs i d’altres que poden ser un èxit total (les situacions intermitges també són habituals, no exagerem). Per això les persones amb qui més comparteixes aquesta fase tenen un significat especial. I és sens dubte el David Requena a qui envïo un dels meus agraïments més especials. Ja fos una matinada de ple hivern a –6ºC o un migdia d’agost coent-nos sobre les pedres, ell mai ha tingut mandra de donar-me un cop de mà. Vam estar de sort el dia que buscaves una font...al Garraf!

El Grup de Recerca de Consolidat 2000SGR00034 de la Universitat de Barcelona és un conjunt gran però una mica difús (quina sort, sinó no sé pas com hi haguéssim cabut al nostre “cubicle”) i està encapçalat per Dr. Nadal i format pel Miquel, la Roser, el Santi, l’Assumpta, la Noèlia, el Lluís, l’Eulàlia, el Jordi, la Diana, el Quim, la Rosa, l’Àlex, el Juli...Gràcies a tots per envoltar (eh! no tots alhora! que no hi cabeu!) aquesta tesi. Amb el permís de la resta, per mi l’Eulàlia i el Miquel es mereixen una menció especial. Amb l’Eulàlia he compartit els mateixos quatre anys de tesi i li dec molt més del que ella mateixa pensa (ja sabeu que l'Eulàlia no acostuma a posar-se pels núvols, però ni cas que els que la coneixeu bé ja sabeu el que val). Del Miquel Borràs me'n duc una impressió molt particular... No és fàcil trobar algú amb qui les converses s'envolten d'una atmosfera tant acollidora. De la resta del Departament de Biologia Animal voldria agrair especialment el suport rebut pel part del seu Director, el Dr. Gosàlbez, que a la vegada és el tutor d'aquesta tesi. No voldria oblidar a cap dels components del Departament que, d'una manera o altre, han col·laborat el aquesta tesi...Gustavo Llorente, Joan Real, Santi Mañosa, Ignasi Torre, Mari Sans, Toni Hernàndez... i molts altres a qui demano una disculpa per no recordar-los en aquest moment.

Si la tesi fos una variable depenent, dins del model de regressió múltiple segur que hi entrarien les aportacions del Pere Pons (destacat reenfocador de la tesi), del Soso (i les seves primeres aportacions estadístiques), d'en Gabriel Gargallo (sí, sí calia fer tres grups d'individus i no dos), Robin Rycroft (more than simple language corrections), Francesc Llimona (han anat força be els point-counts), així com les dels referees Anders Pape Møller, Ken Norris, Jari Kouki, i d'altres a qui també demano disculpes per no recordar-los ara.

Hi ha gent que creu que els biòlegs passem els dies amb uns prismàtics a la mà i unes botes als peus (sovint hi ha una part de la feina que encara és així). Però la realitat quotidiana sol estar molt més a prop de la pantalla del PC que de l'aire lliure. No, no, tranquils, no penso agrair res als ordinadors (us estalviaré el que passa pel meu cap quan es pengen) però si als que sovint m'han ajudat a fer-los "running". Gràcies Víctor, Gràcies Salva.

Gairebé per acabar, voldria fer un poti-poti amb tot un conjunt de gent que també ha estat, d'una manera o altra, al darrera aquesta tesi: Francesc Vila, Constantí Stefanescu, Joan Tàsias, Elena Bisbal, Itziar Pérez, Toni Velasco, Armand Riba, Telm Busquets i Jaume Garganté.

Com és habitual en aquests casos, m'he esperat fins arribar aquí per parlar de la gent que més estimo, aquells sense els quals aquesta tesi, com a part de la meva vida que és, no tindria el sentit que té. Gràcies papes, per haver-me donat la vida i una manera de veure-la. Gràcies Jordi, per haver obert el camí que m'ha portat fins aquí. I, molt especialment, gràcies Olga, per ajudar-me a trobar l'equilibri entre la terra i el cel.

Agraïments oficials

El principal suport econòmic d'aquesta tesi doctoral ha provingut de la beca de Formació de Personal Investigador de del Comissionat per a Universitats i Recerca de la Generalitat de Catalunya. També cal destacar el suport que durant tot el període he rebut del Servei de Parcs Naturals de la Diputació de Barcelona. Durant el 1999, vaig rebre el suport de l'ajut comarcal a la recerca ACOM, atorgat al Museu de Gavà pel Comissionat per a Universitats i Recerca de la Generalitat de Catalunya. El treball inclòs en aquesta tesi forma part de la recerca portada a terme pel Grup de Recerca Consolidat 2000SGR00034 de la Universitat de Barcelona, que ha rebut el suport de CAICYT (PB-96-0224).