

Assessing the response of open-habitat bird species to landscape changes in Mediterranean mosaics

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Received: 16 March 2007 / Accepted: 24 August 2007 / Published online: 14 September 2007
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Abstract In Mediterranean landscapes, wildfires and land abandonment lead to major landscape modifications primarily by favouring the presence of open, shrub-like habitats. At present, we know very little of how these changes affect patterns of species occurrence at the landscape scale. In this work, we analyse the impact of these landscape changes on the occurrence patterns of eight open-habitat species by using presence/absence data collected in the Catalan Breeding Bird Atlas (NE Spain). We compared the species occurrence patterns along habitat gradients for three different landscape settings: a semi-permanent farmland–forest landscape (i.e. with variable proportions of farmland and forests) and two landscape settings which mimic those favoured by land abandonment and fire: farmland–shrubland landscapes and mosaic landscapes (i.e. variable proportions of farmland and forest coexisting with a shrubby matrix). In the forest–farmland landscape, we found a dominant negative effect of adjacent forest on species occurrence rates. This overall effect mostly disappeared in farmland–shrubland landscapes composed by two habitats with more similar vegetation structure. In mosaic landscapes, the general negative effect of forest habitats also appeared to be partially compensated by the presence of a shrubby matrix. Our results suggest that landscape gradients induced by fire and to some degree also land abandonment, mainly favouring availability of shrublands may potentially enhance the resilience of threatened open-habitat species at the landscape scale by increasing the range of potential habitats used. The analysis of species-occurrence patterns along predefined habitat gradients appears as a useful tool to predict potential species responses to land use change.

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Keywords Response curves · Land abandonment · Fire disturbance · Heterogeneity · Landscape context · Habitat selection · Habitat gradient · Open habitat

Introduction

Socioeconomical changes from recent decades have caused the abandonment of less fertile rural areas in many regions of the world including the Mediterranean Basin (Preiss et al. 1997). In these landscapes, the abandonment of traditional agricultural activity leads to secondary succession and vegetation development which increases in turn the amount of shrubland and forests at the landscape scale (Escarré et al. 1983; Masalles and Vigo 1987, Farina 1997; Sirami et al. 2007). In many areas affected by land abandonment, fire is rapidly becoming the main cause of large-scale habitat disturbance and a major agent maintaining availability of open habitats and landscape heterogeneity by turning forest into shrublands (Moreira et al. 2001; Lloret et al. 2002).

In this context, habitat changes induced by land abandonment and fire are expected to be critical in determining future biodiversity patterns in large areas of the Mediterranean Basin (Preiss et al. 1997; Moreira et al. 2001; Herrando et al. 2003; Sirami et al. 2007). For birds in particular, such changes may be especially important since several open-habitat species have begun to decline alarmingly in the recent years and many of them are now of particular European conservation concern (BirdLife International 2004).

Recent evidences suggest that the way habitats integrate the landscape may be a key factor in determining species occurrence patterns (Tiainen and Pakkala 2001; Fuller et al. 2004; Brotons et al. 2005a, b). Therefore, studies dealing with bird–landscape relationship should not recognise habitat patches embedded within completely unsuitable habitat, as has been postulated by the applications of the island biogeography theory (MacArthur and Wilson 1967), but consider the complexity of heterogeneity in habitat mosaics (Virkkala et al. 2004). In dynamic, mosaic landscapes such as Mediterranean landscapes, habitat patches are not likely to be perceived by animals as discrete units in the landscape (Wiens 1994), but rather species will show a gradual range of affinity for different habitats or combination of habitats (Dunning et al. 1992; Brotons et al. 2005b)

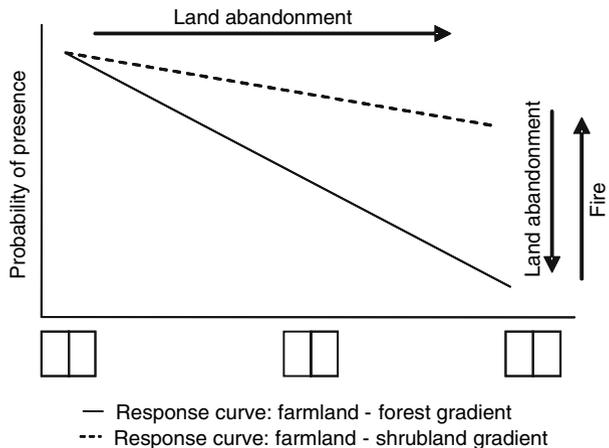
The distribution of open-habitat bird species will be mainly determined by their ability to respond to landscape changes and to colonise new originated habitats. A number of studies have shown significant decreases of open-habitat bird species under a land abandonment context (Preiss et al. 1997; Sirami et al. 2007) whereas these species may be benefited by the impacts derived from the occurrence of wildfires (Pons and Prodon 1996; Herrando et al. 2003). However, further approaches at a landscape scale are needed to assess the processes underlying changes in occurrence patterns in dynamic Mediterranean landscapes. An interesting approach to solve this gap in knowledge is the comparative analysis of species occurrence patterns along environmental gradients (i.e. species response curves along habitat gradients) in different landscape settings expected to be created by the dynamics behind land use changes, as for instance land abandonment and fire disturbance (Fig. 1) (Andrén et al. 1997). In this context, the continuum model (Austin 1999) is being taken into consideration through the definition of habitat gradients and creates an explicit link between species' distribution patterns and ecological processes (Fischer and Lindenmayer 2006). Most of the studies about response curves along an ecological gradient have been conducted on plant species (Austin 2002; Oksanen and Minchin 2002;

Rydgren et al. 2003; Coudun and Gegout 2005; Yee 2006) and relatively little research has focused on response curves for animals describing ecological processes at the landscape scale (Suárez-Seoane et al. 2002).

The aim of this work was to study the occurrence patterns of eight open-habitat species with different habitat preferences, in different landscapes mimicking habitat arrangement arising from land abandonment–fire impact dynamics. With this purpose in mind, we used three different landscape settings: (1) Farmland–forest landscapes, which was used as reference landscape, covered with a stable mixture of semi-permanent open habitats (farmland) and well developed vegetation areas (forests). We consider this gradient as a hypothetically future landscape in case of long-term land abandonment and total fire suppression favouring forest habitat as the dominant natural vegetation with variable farmland proportion (Farina 1997; Sirami et al. 2007). The transition from farmland to forest defines a habitat gradient characterized by a heavy sharp contrast of vegetation structure between habitat patches. (2) Farmland–shrubland landscape which emulate the habitat combination emerging from convergent driving forces into the landscape: short-term land abandonment and fire which leads to different degrees of coexisting open habitats (Fig. 1). Its correspondent habitat gradient is characterized by a soft contrast between habitat patches. (3) Mosaic landscape in which farmland and forest coexist with a shrubby matrix habitat. This gradient may be interpreted as a surrogate of the heterogeneous landscape more commonly created after fire impact (Romme 1982; Lloret et al. 2002).

We mimicked hypothetical changes in these landscape settings by performing comparisons of the species response curves along habitat gradients between two different landscape settings: (a) the farmland–forest with the farmland–shrubland landscape; (b) the farmland–forest with a mosaic landscape. We then addressed the following two hypotheses. First, landscape changes associated to short-term land abandonment and fire favour the coexistence of different open habitats (farmland and shrubland) leading to softer vegetation contrast between dominant habitat types. In this case, we expect an increase in the range of habitat combinations used by our focal species in farmland–shrubland dominated landscapes when compared to a farmland–forest landscape. We also expect, that landscape changes related to long-term abandonment and fire suppression that favour the conversion of shrubland into forest, will affect negatively open-habitat species occurrence

Fig. 1 Conceptual model representing the species’ response curves along different habitat gradients. Habitat gradients will be modified according to the main driving forces in large-scale landscape dynamics: land abandonment and fire. In this conceptual model only linear responses are shown as simple examples of response curves along two compared habitat gradients



patterns. Second, we hypothesized that mosaic landscapes will affect the processes of habitat selection by inducing interactions among the coexisting habitats (i.e. farmland, shrubland and forest). The effect of nearby habitats on species occurrence has been recognised as an important issue (Sisk et al. 1997; Virkkala et al. 2004; Fuller et al. 2004; Brotons et al. 2005b) and could potentially provide critical insights into species response to landscape changes. With the presence of a shrubby matrix habitat, species may be able to use a wider range of habitats and benefit from their coexistence in the landscape. If this hypothesis holds true, species acquiring resources from adjacent habitats or with strong preference for the combination of shrubland with other habitats (i.e. farmland or forest) in the landscape will show an increase in their occurrence patterns along the examined habitat gradients.

Material and methods

Study area

The study was carried out in Catalonia (31.930 km²), which is situated in the north-east of the Iberian Peninsula and has a typically Mediterranean climate (between c. 0°15' E and 3°20' E longitude and 40°30' N and 42°40' N latitude). Landscape changes related to socio-economical dynamics in this region may be representative of those that occurred in the whole Mediterranean Europe during the last decennia: increases in land abandonment that leads to fuel accumulation and therefore an increase in wildfire impact (Le Houerou 1990), which reveal two opposing forces driving large-scale landscape dynamics (Fig. 1). In this context, open-vegetation habitats like shrublands in our study area arise mainly through secondary succession after abandonment of less productive cropland and fire. Either originated from land abandonment or fire, shrubby formations in our study area appear to be structurally similar and mainly dependent on local environmental conditions and land use history (Calvo et al. 2002; Pérez et al. 2003).

Between 1975 and 2000 the forest cover increased throughout Catalonia by about 225,000 ha (Gil et al. 2005). This increase is surprising because during this period about 234,000 ha of forests and shrublands were burned (Diaz-Delgado et al. 2004). In spite of the great impact of wildfires and the agricultural abandonment of less productive areas (c. 100,000 ha in the last 20 years), the shrubby vegetation has decreased by more than 200,000 ha (Gil et al. 2005), as a consequence of secondary succession following land abandonment leading to the development of forest formation.

Bird occurrence data

This work focused on eight bird species characterised by their different degree of specialization on open habitats with variable preferences for shrubland and dry, extensive farmlands (Estrada et al. 2004): *Alectoris rufa*, *Anthus campestris*, *Carduelis cannabina*, *Emberiza calandra*, *Emberiza hortulana*, *Galerida theklae*, *Lullula arborea* and *Oenanthe hispanica*. These species also have been shown in previous studies to be especially abundant on post-fire areas in Catalonia (Pons and Prodon 1996; Herrando et al. 2002). We selected these species because they may be benefited in a different way from landscape changes affecting open habitats such as farmland and shrubland.

Data on species occurrence patterns in different landscapes were obtained from the Catalan Breeding Bird Atlas (CBBA, Estrada et al. 2004). The CBBA is a large-scale survey that covered between 1999 and 2002 the whole of the Catalonia using a grid based 10 km Universal Transverse Mercator (UTM) squares. A total of 3,077 1 km squares (approximately 9% of the total area) were selected to conduct standardised intensive surveys of species presence in a stratified fashion to cover the main habitat types present within each of the 10 km squares (Hirzel and Guisan 2002). Two 1-h surveys were conducted for each one of the selected UTM 1×1 km squares during which every square was entirely surveyed and every detected species recorded.

Habitat gradients

For the purpose of this study, habitat was considered as a spatially contiguous and homogeneous vegetation type that appears to be physiognomically distinctive from other categories (i.e. land-cover, Hutto 1985). We derived the cover of the three considered habitats (farmland, shrubland and forest) for each of the 3,077 1 km squares sampled in the CBBA, using the Catalan land use map (1997) originated from remote sensing imagery (Viñas and Baulies 1995). We defined three landscape settings by selecting the 1×1 km squares for which the sum of the habitats considered was dominant (>75% of the square surface). In this way, we defined the farmland–forest landscape corresponding to the squares with a sum of two habitats higher than 75% (1,405 squares). Following the same reasoning, 1,367 squares were assigned to the farmland–shrubland landscape setting, and finally 509 squares to the mosaic landscape setting. In the case of latter, we selected squares for which the sum of the three habitats was also greater than 75% of the total square surface but shrubland was present in all squares with a proportion ranging between 25% and 50% of the total formed by the three habitats.

Finally, for each of these three landscape settings the selected 1×1 km squares were classified in 20 different ranges corresponding to different landscape classes with similar relative habitat composition. Each class contained a minimum of 10 1×1 km squares. The landscape classes were arrayed along habitat gradients expressing the decrease in farmland proportion across the landscape in relation to the alternative habitat. In order to test hypothesis one, we compared farmland–forest with farmland–shrubland landscapes, whereas to test hypothesis two (i.e. evaluate the effect of the shrubby matrix); we compared the gradient of decreasing farmland proportion in relation to forest between the reference (farmland–forest) and the mosaic landscapes.

Statistical analysis and test of landscape ecological processes

For each species we estimated mean occurrence rate within each landscape class by averaging the number of presences. We obtained information on the shape of the responses by analysing patterns of species occurrence for the different landscape classes along the habitat gradient performing simple stepwise regression models (Zar 1998). To this end, we included the first and second order polynomial of the habitat gradient to test for different landscape ecological processes (Table 1) based on the statistical significance of the linear and quadratic term (P -value <0.05) and the sign of their coefficients corresponding with different shapes of response curves (Table 1) (Appendix)

After the estimation of the shape of the species response curve for each habitat gradient (Fig. 2), we proceeded to their comparison between landscape settings. Here we tested whether significant differences existed between response curves by including landscape setting into the regression model.

To quantify changes in occurrence patterns originated by landscape changes, we compared species occurrence rates along two habitat gradients whenever they were statistically different. The change in occurrence patterns between the compared landscapes indicates a different degree of response to landscape changes. As the response curves along the compared habitat gradients approach, the area between the curves tends to decrease. This may be interpreted in terms of a reduced impact of landscape changes on species occurrence. However, since the area between curves is likely to be influenced by the total abundance of a given species (i.e. species highly abundant are susceptible to suffer higher change in occurrence patterns); we estimated the change in occurrence patterns related to the mean probability of presence (defined from here onwards as ‘landscape-changes response’, LCR). In this way, LCR was calculated by dividing the area between two response curves (estimated through integration curves) by the mean probability of presence along both compared gradients according to Eq. 1. We were able to estimate the relative importance of the species response to landscape changes occurred between the two gradients, having an accumulative measure of the species response along the whole gradient through integration curves.

$$\text{LCR} = \int_0^1 [(R_{c1}) - (R_{c2})] dx \times P^{-1} \quad (1)$$

where R_c represents the function describing variations in species occurrence patterns along a given gradient (response curve) and being $R_{c1} \geq R_{c2}$. And P corresponds to the mean probability of presence for the habitat gradients compared.

Table 1 Summary of the possible shape of responses determined by the relationship between species occurrences and habitat composition along a given habitat gradient as shown in Fig. 2

	Response to habitat gradients			
	Linear term		Quadratic term	
	Coefficient sign	<i>P</i> -value	Coefficient sign	<i>P</i> -value
Habitat loss ^a	Negative	$P < 0.05$	(–)	n.s.
Partial compensation ^b	Negative	$P < 0.05$	(–)	n.s.
Perfect compensation	(–)	n.s.	(–)	n.s.
Fragmentation	Negative	$P < 0.05$	Positive	$P < 0.05$
Supplementation	Negative	$P < 0.05$	Negative	$P < 0.05$
Complementation	(–)	n.s.	Negative	$P < 0.05$

Statistical recognition of the shape for a given species response curve was derived from the assessment of the coefficients (linear and quadratic terms) of the regression model relating mean species occurrence rate for a given habitat gradient (decrease in farmland proportion in relation to an alternative habitat in the landscape)

^a If the coefficient sign is positive, the identified response will be same but corresponding to the non-farmland habitat

^b It differs from the ‘habitat loss’ in that the probability of presence in the habitat where the species is less abundant is different from zero (considering the 95% confidence intervals)

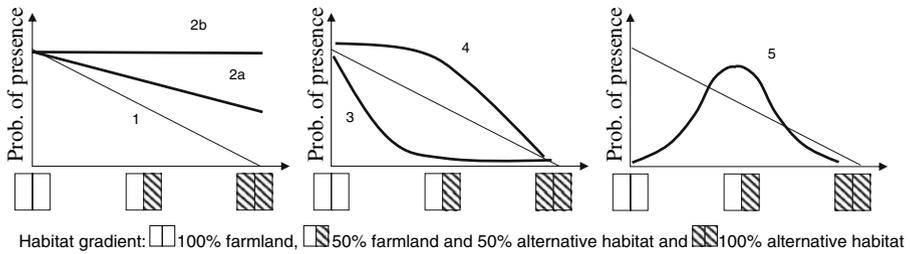


Fig. 2 Ecological processes of habitat selection at a landscape scale according to five types of response curves along habitat gradients: (1) ‘Habitat loss’: species occurrence decreases in the same proportion as the preferred habitat (i.e. habitat with higher occurrence rate). (2a) ‘Partial compensation’: species compensate the loss of the preferred habitat by using low quality adjacent habitats (Norton et al. 2000); (2b) ‘Perfect compensation’: species does not perceive changes in habitat quality between the two habitats; (3) ‘Fragmentation’: adjacent habitat offers no resources to the species and has a negative effect on the species present in the preferred habitat. (4) ‘Supplementation’: species obtains resources from adjacent habitat supplementing those found in the preferred habitat. (5) ‘Complementation’: species requires complementary resources present in adjacent habitats, thus showing a peak of species occurrence when the two habitats coexist. Modified from Andrén et al. 1997; Brotons et al. 2005b

Results

Response curves along two-habitat landscape gradients

The species included in this study showed a diversity of responses to the habitat gradients analysed leading to a variety of response curves. Along the farmland–forest gradient, which has a sharp contrast in vegetation structure between the two habitats, the dominant ecological processes detected in species habitat selection were ‘fragmentation’ and ‘habitat loss’ (Table 2). For three species supporting ‘fragmentation’ type responses (*A. rufa*, *G. theklae* and *O. hispanica*), the decrease in occurrence rates along the gradient decreased more rapidly as forest habitat increased in the landscape than expected by ‘habitat loss’. Other three species (*C. cannabina*, *E. calandra* and *E. hortulana*) showed decreases in occurrence proportional to increases in forest habitat, and thus matched the process of ‘habitat loss’. Finally, the occurrence patterns of two species (*L. arborea* and *A. campestris*) fitted the ‘perfect compensation’ type response showing no significant differences in occurrence rates as the proportion of forests changed along the gradient (Table 2). We should also note here, that *A. campestris* was virtually absent from the farmland–forest landscape setting.

In contrast to the farmland–forest gradient, along the farmland–shrubland gradient none of the species considered showed a negative, non-linear effect, of increasing shrubland habitat on occurrence patterns. Along this gradient, four species were present at both ends of the gradient but being more common at one of them, thus matching the ‘partial compensation’ process of habitat selection (Fig. 3). Three of these species (*C. cannabina*, *E. hortulana* and *A. campestris*) were observed more frequently in shrublands, whereas *E. calandra* preferred farmland dominated landscapes but also used to a large extent shrubland dominated ones. Three species (*A. rufa*, *O. hispanica* and *G. theklae*) matched the ‘perfect compensation’ process along the farmland–shrubland gradient, showing the similar occurrence rates for the whole extent of the gradient. Finally, *L. arborea* exhibited a bell shaped response curve fitting the predictions of the ‘complementation’ response by

Table 2 Summary of the shape of species response curves along a habitat gradient (i.e. type of response) in reference (farmland–forest) and open-habitat landscapes (farmland–shrubland)

Species	Type of response along habitat gradient		LCR ^a	P. trends ^b
	Farmland–forest	Farmland–shrubland		
<i>A. rufa</i>	Fragmentation	Perfect compensation	0.79	No change
<i>A. campestris</i>	Perfect compensation	Partial compensation	1.58	+88%
<i>C. cannabina</i>	Habitat loss	Partial compensation	0.74	No change
<i>E. calandra</i>	Habitat loss	Partial compensation	0.41	–5%
<i>E. hortulana</i>	Habitat loss	Partial compensation	1.58	+82%
<i>G. theklae</i>	Fragmentation	Perfect compensation	1.47	+44%
<i>L. arborea</i>	Perfect compensation	Complementation	0.34	+20%
<i>O. hispanica</i>	Fragmentation	Perfect compensation	1.22	–20%

'Landscape-changes response' (LCR) indicates the changes in occurrence patterns between the compared habitat gradients. See also Table 1

^a We estimated 'landscape-changes response' as the changes in occurrence patterns between the two compared habitat gradients (calculated as the area between curves through curve integration, see methods) related to the mean probability of presence for both compared landscapes

^b Population trends: percentage of population increase(+)/decrease (–) in Catalonia during the last 20 years (Estrada et al. 2004)

being favoured by the coexistence of both open habitats (i.e. farmland and shrubland) (Table 2; Fig. 3).

When we estimated differences in overall occurrence patterns between the two landscape settings, all studied species showed a significant overall increase in occurrence rates from the reference farmland–forest to the farmland–shrubland setting (Fig. 3). However, 'landscape-changes response' (LCR) showed an idiosyncratic behaviour among the species. When we compared LCR between landscapes, the species that underwent the largest relative change were *E. hortulana*, *A. campestris* and *G. theklae* (Table 2). This indicated a relatively higher benefit from the formation of associated open-habitats landscape (farmland and shrubland) on these species. Conversely, *E. calandra* and *L. arborea* were the species with smallest response to these landscape changes.

Effect of shrubby matrix presence in a farmland–forest landscape

In mosaic landscapes, four species compensated decreases in farmland habitat as forest increased in the presence of a shrubby matrix (Fig. 4). The other four species (*A. rufa*, *E. calandra*, *G. theklae* and *O. hispanica*) did not occupy forest dominated landscapes even in event of the presence of a shrubby matrix, supporting the 'habitat loss' response (Fig. 4).

However, for these species, except for *E. calandra* (*P*-value landscape setting >0.05), the presence of such a shrubby matrix reduced the 'fragmentation' effect observed in the reference farmland–forest landscape by smoothing the decrease in species mean occurrence as the proportion of forests increased in the landscape. For *C. cannabina* and *L. arborea*, the mosaic landscape contributed to an overall increase in occurrence rates across the gradient supporting a compensating effect of the shrubland habitat in mosaic landscapes (Table 3). In case of significant differences between both landscape settings, the species with greatest LCR were, *G. theklae*, *C. cannabina* and *O. hispanica* (Table 3),

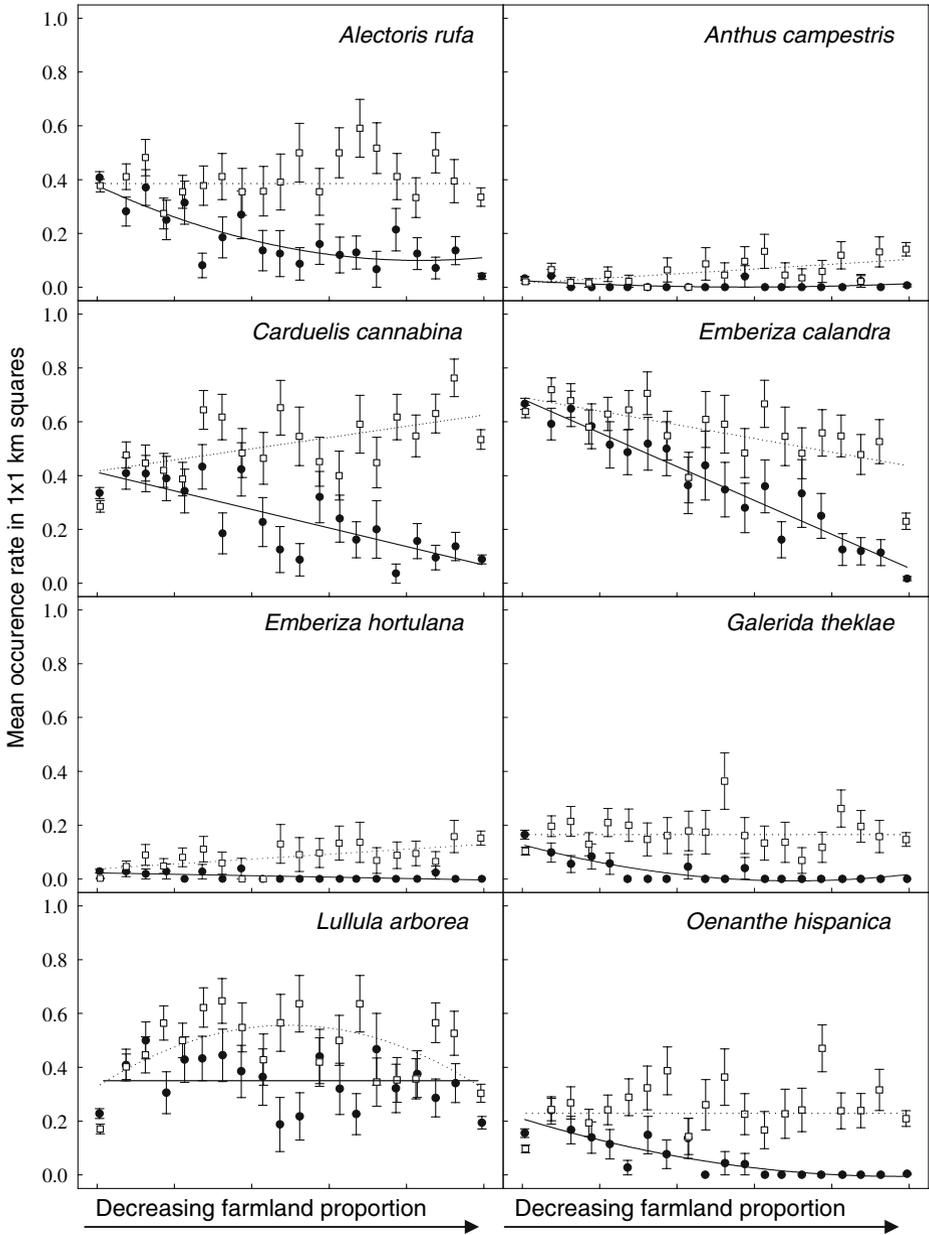


Fig. 3 Response curves for the eight studied bird species along the compared habitat gradients: farmland–forest (black circles and black line) and farmland–shrubland (white squares and dotted line). Vertical bars represent the standard error of the mean. All compared response curves were significantly different (landscape setting P -value <0.05)

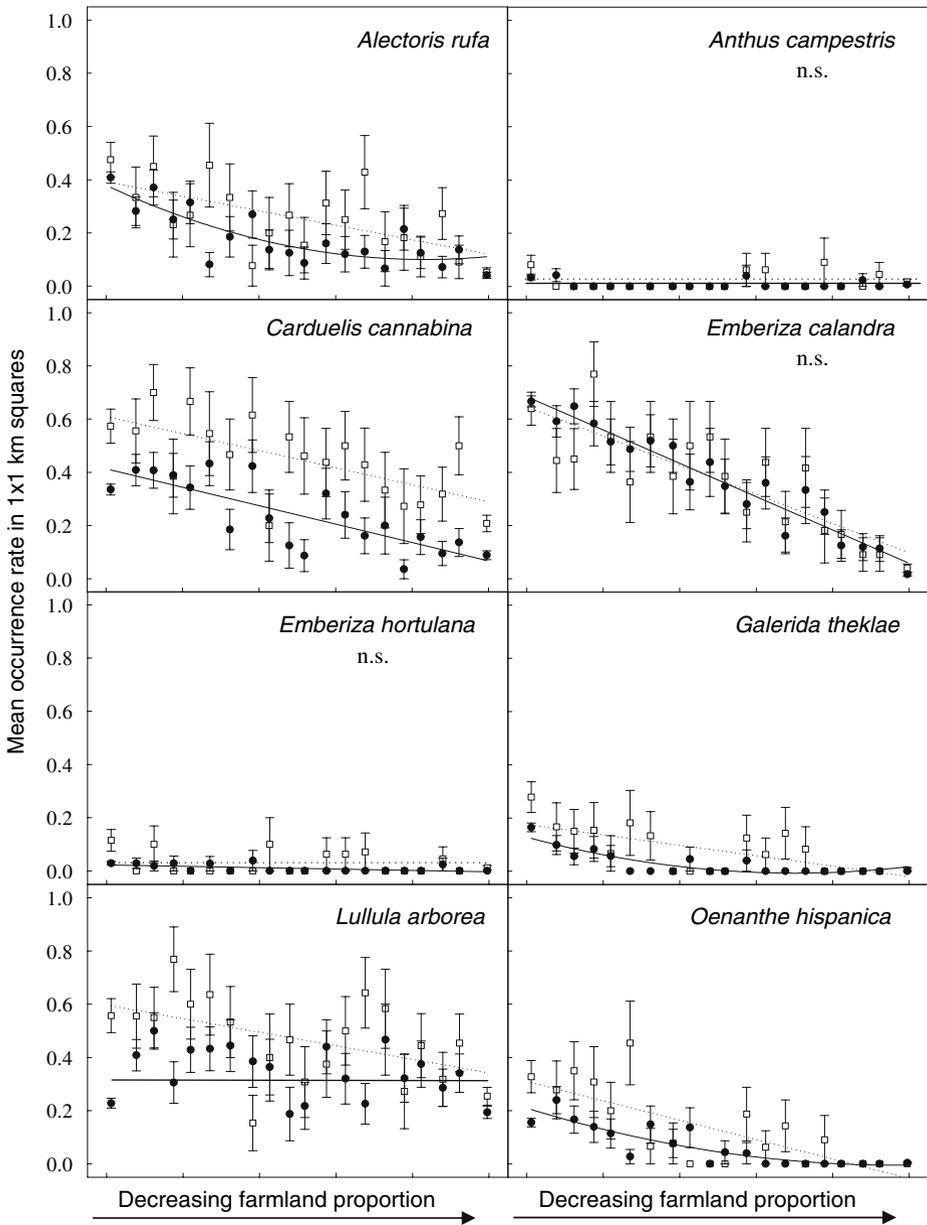


Fig. 4 Response curves along the farmland–forest gradient for the 8 studied species in two compared landscape settings: the farmland–forest (black circles and black line) and the mosaic landscape (white squares and dotted line). Vertical bars represent the standard error of the mean. No significant differences between response curves are indicated with n.s. under the species name

Table 3 Summary of the shape of species response curves along a habitat gradient (i.e. type of response) in mosaic landscapes

Species	Mosaic landscape		'Landscape-changes response' ^a
	Equation ^b	Type of response along habitat gradient	
<i>A. rufa</i>	0.39–0.27grad	Habitat loss	0.37
<i>A. campestris</i>	0.01	Perfect compensation	n.s.
<i>C. cannabina</i>	0.61–0.32grad	Partial compensation	0.64
<i>E. calandra</i>	0.65–0.55grad	Habitat loss	n.s.
<i>E. hortulana</i>	0.04	Perfect compensation	n.s.
<i>G. theklae</i>	0.18–0.20grad	Habitat loss	0.95
<i>L. arborea</i>	0.60–0.26grad	Partial compensation	0.20
<i>O. hispanica</i>	0.31–0.36grad	Habitat loss	0.63

'Landscape-changes response' indicates the change in occurrence patterns when comparing the reference landscape (farmland–forest) with the mosaic landscape. See also Table 1

^a We estimated 'landscape-changes response' as the changes in occurrence patterns between the two compared gradients (calculated as the area between curves through curve integration, see methods) related to the mean probability of presence for both compared landscape settings

^b Only significant coefficients are represented

undergoing the largest increase in their occurrence rates in relative terms. These species appear thus, to be the most benefited from the formation of mosaic landscapes associated to forests, farmland and shrubland. In contrast, two later, scarcer species, *A. campestris* and *E. hortulana*, showed a similar preference for farmland and forest irrespectively of the landscape setting (P -value landscape setting >0.05). Finally, at the scale analysed, our results provided no evidence for the supplementation process to play any significant role for the species analysed in any of the landscape settings.

Discussion

Our study strongly supports the view that landscape changes in the habitat mosaic favouring the coexistence between open-habitats favour the set of species analysed. The analysis of species response curves provides essential information relative to the processes of habitat selection at the landscape scale. The comparison of the occurrence patterns in farmland–forest landscapes with those related to the shrubland dynamics in the landscape (farmland–shrubland and mosaic landscapes) allowed confirming that bird species were greatly favoured by the presence of shrubland habitats and by the formation of habitat mosaic landscapes analogous to those potentially originated by fire and land abandonment. However each species responded in an idiosyncratic way to the habitat gradients analysed, given their different degree of specialization on the habitats considered in this study (Fuller et al. 2004).

In a farmland–forest landscape, most of our focal open-habitat species were negatively affected by the increasing proportion of forest habitat, therefore the 'fragmentation' and 'habitat loss' processes appear to primarily drive species responses to habitat changes (Andrén et al. 1997). Instead, in farmland–shrubland landscapes favoured by land abandonment and/or fire, processes in which open-habitat species acquire resources from both habitats (farmland and shrubland) seem to dominate (Norton et al. 2000). The similarity of

vegetation structure among these two habitats was probably the reason under the increase in the probability of presence along the whole gradient when comparing with the farmland–forest. Coexistence between open habitats involves more flexible processes of habitat selection for open-habitat species. Similarity in vegetation structure of major habitat features has been already pointed out by some authors as a key factor in habitat selection (Donald et al. 2001; Brotons et al. 2005b).

Heterogeneous landscapes also favoured the increase in the occurrence patterns of most of the species when comparing with the reference farmland–forest landscape, but no for *A. campestris*, *E. calandra* and *E. hortulana*. The presence of a shrubby matrix habitat increased the occurrence patterns of the species when coexisting with farmland and also decreased the negative effect of forest habitat on open-habitat species occurrence as forest proportion increases. The species which largely smoothed the negative effect of forest with the presence of a shrubby matrix (i.e. *G. theklae* and *O. hispanica*) underwent the largest increase in occurrence patterns. Contrary to our expectations not all species acquiring resources from adjacent habitats or with strong preference for mosaic landscapes (i.e. *L. arborea*) showed a large response to landscape changes. The wide range of habitats used, which makes the species more resilient to habitat changes (Gage et al. 2004; Charrette et al. 2006), may explain such a response (Andr n et al. 1997).

In the light of our results, the coexistence of habitat types in heterogeneous landscapes created by perturbation dynamics appears as a determinant factor in habitat selection processes of open-habitat species (Norton et al. 2000). The wider range of habitats used in heterogeneous landscapes (i.e. mosaic landscape) might favour the species ability to cope with landscape changes. This species resilience to habitat changes might decrease sensitivity to variations in the amount available habitats (Moreira et al. 2001), leading to more stable populations under a changing landscape context. As it was shown by Scozzafava and De Sanctis (2006) the hedgerow removal in the last decades by modern agriculture is causing many farmland bird species to contract back to shrublands and woodlands edges. In accordance with our results, this response was not clearly supported for *E. calandra* (Scozzafava and De Sanctis 2006). Therefore species with narrow range of habitats used are likely to experience smaller responses to landscape changes because they respond mostly to changes in their preferred habitat.

Landscape heterogeneity favours the range of used habitats; therefore, it seems to become crucial for the maintenance of open-habitat species (Brotons et al. 2005a). On one hand, the preservation of suitable open habitats within a mosaic landscape may enhance colonization capabilities of species after forest fires (Frouz and Kindlmann 2001; Murphy 2001). On the other hand, forest habitats may act as barriers to species movements (Mayr 1963), having a potential negative effect on species distribution. However, for most of the species under study, ‘partial compensation’ processes appeared to increase the permeability of such barriers when a shrubby matrix was present. This was probably due to the formation of smooth boundaries (i.e. similar vegetation structures in adjacent habitats) which may facilitate movement between dominant habitat types in landscapes generated by short-term land abandonment and fire dynamics (Forman 1995).

Species distribution trends and responses to landscape changes

The analysis of species–occurrence patterns along predefined habitat gradients may offer a useful tool to predict species responses to land use change. Our approach based on the comparison of the occurrence patterns along different habitat gradients could be also

applied as a proxy to evaluate the potential impact of other prevailing landscape changes such as agricultural intensification or urbanization.

The distribution area of *A. campestris*, *E. hortulana* and *G. theklae* trends to increase during the last 20 years in Catalonia (Table 2; Estrada et al. 2004). This increase was mainly related to the colonization of new areas affected by fire in recent years (Estrada et al. 2004) that favours the availability of coexisting open habitats. Pons and Prodon (1996) have shown that at local scale, in Mediterranean regions, these species colonize or increase notably their populations after fire. At the landscape scale, these species showed a strong ‘compensation effect’ when a farmland–forest landscape was compared to a farmland–shrubland landscape, suggesting that the species are likely indeed to benefit from the coexistence of open habitats. In spite of the global decrease of shrubland habitats in Catalonia during the last two decades (Gil et al. 2005), a relevant local increase of open-shrubland habitats has been described in central Catalonia. This local increase is likely to be induced by the effects of farmland abandonment and specially the impact of fire in large areas (Diaz-Delgado et al. 2004), which benefit the species mentioned before. The increase of the distribution area for *A. campestris* and *E. hortulana* is especially relevant given their large scale negative population trends elsewhere in Europe (BirdLife International 2004). Although knowing the certain causes of migrant population decline is not easy (Sanderson et al. 2006), habitat changes are therefore probably linked to the increase of the distribution area of these species in Catalonia.

In case of other migrant species of European conservation concern such as *O. hispanica*, for which we may predict an increase of species distribution because of its large LCR, the distribution area in Catalonia has diminished by about 20% (BirdLife International 2004). Although this species is known to colonize recent burned areas (Pons and Prodon 1996), for *O. hispanica* other factors than large scale landscape changes might drive species distribution trends and also its population (i.e. drought in wintering areas, Mestre et al. 1987). Complementary scale approaches are needed to quantitatively assess habitat specific changes in order to unambiguously unravel specific causes of species distribution changes. *E. calandra*, which also showed a strong preference for farmland, probably appears as another example of stronger dependence on local factors concerning changes in farmland habitat quality, such as agricultural intensification. In this case, changes in farmland rather than availability of new habitats may probably have had a proportional larger contribution to the overall species distribution trends (Fuller et al. 1995; Donald et al. 2001; Gregory et al. 2004).

Conclusions

The large influence of the landscape context on open-habitat bird communities (Blondel and Farré. 1988; Virkkala et al. 2004; Brotons et al. 2005b) has been corroborated by this study. The results demonstrate that the coexistence of farmland and shrubland benefit open-habitat bird species, even in the case of species showing higher relative preferences for farmland habitats (Fuller et al. 2004). In most cases, the presence of a shrubby matrix in mosaic landscapes also decreases the negative effect of forest habitat on open-habitat species distribution. Furthermore mosaic landscapes can also provide suitable habitat for forest bird species, given that shrubland seems to be permeable to some degree for these species (Herrando and Brotons 2002). Hence, the maintenance and even the enhancement of bird diversity at the landscape scale in Mediterranean regions may depend on the preservation of a mosaic of habitats where fire is expected to play an active role (Piñol et al. 1998; Moreira et al. 2001).

However, when considering interactions between adjacent habitats, it is important to account for temporal variability in composition at the landscape scale (Forman 1995). These landscape changes cause species-specific ecological processes that should be also taken into consideration. The transitional character of shrubland habitats may limit the benefits of land abandonment and fire for open-habitat species at the landscape scale (Prodon et al. 1987). In this case, population decreases will be expected for all the species, especially for those which the habitat ‘fragmentation’ and ‘habitat loss’ processes arose, in case that succession takes the lead in driving vegetation dynamics. For this reason the transitional character of shrublands must be taken into consideration for landscape planning and development of animal conservation policies.

Acknowledgements We thank all volunteers that participated in the Catalan Breeding Bird Atlas (CBBA). This work is a contribution to the European Research Group GDRE “Mediterranean and mountain systems in a changing world” and has received financial support from the project CGL2005-00031/BOS granted by the Spanish Ministry of Education and Science and has been supported by a Marie Curie International Reintegration grant within the 6th European Community Framework programme. L.B. benefited from a Ramon y Cajal contract from the Spanish government and S.V. (FI fellowship) received financial support from the Departament d’Universitats, Recerca i Societat de l’Informació de la Generalitat de Catalunya and Social European Fund Department.

Appendix

Regression coefficients of the response curves for each of the three landscape settings for the studied species

Species	Constant	Linear term	Quadratic term	Model <i>P</i> -value
Farmland–forest landscape				
<i>A. rufa</i>	0.38	−0.67	0.40	<0.001
<i>A. campestris</i>	0.01	n.s.	n.s.	n.s.
<i>C. cannabina</i>	0.41	−0.35	n.s.	<0.001
<i>E. calandra</i>	0.69	−0.63	n.s.	<0.001
<i>E. hortulana</i>	0.02	−0.03	n.s.	0.010
<i>G. theklae</i>	0.13	−0.38	0.27	<0.001
<i>L. arborea</i>	0.34	n.s.	n.s.	n.s.
<i>O. hispanica</i>	0.21	−0.44	0.23	<0.001
Farmland–shrubland landscape				
<i>A. rufa</i>	0.41	n.s.	n.s.	n.s.
<i>A. campestris</i>	0.01	0.09	n.s.	0.007
<i>C. cannabina</i>	0.42	0.21	n.s.	0.013
<i>E. calandra</i>	0.69	−0.26	n.s.	0.001
<i>E. hortulana</i>	0.04	0.09	n.s.	0.008
<i>G. theklae</i>	0.17	n.s.	n.s.	n.s.
<i>L. arborea</i>	0.33	0.92	−0.93	0.034
<i>O. hispanica</i>	0.26	n.s.	n.s.	n.s.
Mosaic landscape				
<i>A. rufa</i>	0.39	−0.27	n.s.	0.003
<i>A. campestris</i>	0.02	n.s.	n.s.	n.s.
<i>C. cannabina</i>	0.61	−0.32	n.s.	0.002

Appendix continued

Species	Constant	Linear term	Quadratic term	Model <i>P</i> -value
<i>E. calandra</i>	0.65	−0.55	n.s.	<0.001
<i>E. hortulana</i>	0.03	n.s.	n.s.	n.s.
<i>G. theklae</i>	0.18	−0.20	n.s.	0.001
<i>L. arborea</i>	0.60	−0.26	n.s.	0.027
<i>O. hispanica</i>	0.31	−0.36	n.s.	<0.001

Significance of the linear and the quadratic term were judged according to the results of a linear regression model (*P*-value <0.05)

'n.s.' no significant term *P*-value >0.5

References

- Andrén H, Delin A, Seiler A (1997) Population response to landscape changes depends on specialization to different landscape elements. *Oikos* 80(1):193–196
- Austin MP (1999) A silent class of paradigms: some inconsistencies in community ecology. *Oikos* 86:170–178
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol Modell* 157(2–3):101–118
- BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge, UK (BirdLife Conservation Series No. 12)
- Blondel J, Farré H (1988) The convergent trajectories of bird communities in European forests. *Oecologia* 75:83–93
- Brotons L, Pons P, Herrando S (2005a) Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *J Biogeogr* 32:789–798
- Brotons L, Wolff A, Paulus G, Martin JL (2005b) Effect of adjacent agricultural habitat on the distribution of passerines in natural grasslands. *Biol Conserv* 124:407–414
- Calvo L, Tarrega R, De Luis E (2002) The dynamics of Mediterranean shrubs species over 12 years following perturbations. *Plant Ecol* 160(1):25–42
- Charrette NA, Cleary DFR, Mooers AO (2006) Range-restricted, specialist bornean butterflies are less likely to recover from enso-induced disturbance. *Ecology* 87:2330–2337
- Coudun C, Gegout JC (2005) Ecological behaviour of herbaceous forest species along a pH gradient: a comparison between oceanic and semicontinental regions in northern France. *Glob Ecol Biogeogr* 14(3):263–270
- Diaz-Delgado R, Lloret F, Pons X (2004) Spatial patterns of fire occurrence in Catalonia, NE, Spain. *Landsc Ecol* 19(7):731–745
- Donald PF, Evans AD, Buckingham DL, Muirhead LB, Wilson JD (2001) Factors affecting the territory distribution of Skylarks *Alauda arvensis* breeding on lowland farmland. *Bird Study* 48:271–278
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175
- Escarré J, Houssard C, Debussche M (1983) Évolution de la végétation et du sol après abandon cultural en région méditerranéenne: étude de succession dans les Garrigues du Montpelliérais (France). *Acta Oecol* 4(5):221–239
- Estrada J, Pedrocchi V, Brotons L, Herrando S (eds) (2004) *Atles dels ocells nidificants de Catalunya 1999–2002*. Institut Català d'Ornitologia (ICO)/Lynx Edicions, Barcelona
- Farina A (1997) Landscape structure and breeding bird distribution in a sub-Mediterranean agro-ecosystem. *Landsc Ecol* 12:365–378
- Fischer J, Lindenmayer BD (2006) Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos (Forum)* 112(2):473–480
- Forman RTT (1995) *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press
- Frouz J, Kindlmann P (2001) The role of sink to source re-colonisation in the population dynamics of insects living in unstable habitats: an example of terrestrial chironomids. *Oikos* 93:50–58

- Fuller RJ, Gregory RD, Gibbons DW, Marchant JH, Wilson JD, Carter N (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conserv Biol* 9:1425–1441
- Fuller RJ, Hinsley SA, Swetnam RD (2004) The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. *Ibis* 146(2):22–31
- Gage GS, Brooke MD, Symonds MRE, Wege D (2004) Ecological correlates of the threat of extinction in Neotropical bird species. *Anim Conserv* 7:161–168
- Gil L, Casals V, Pardo F, Xalabarder M, Postigo JM (2005) Tercer Inventario Forestal Nacional. La transformación histórica del paisaje forestal en Cataluña. Ministerio de Medio Ambiente
- Gregory RD, Noble DG, Custance J (2004) The state of play of farmland birds: population trends and conservation status of lowland farmland birds in the United Kingdom. *Ibis* 146:1–13
- Herrando S, Brotons L (2002) Forest bird diversity in Mediterranean areas affected by wildfires: a multi-scale approach. *Ecography* 25(2):161–172
- Herrando S, Brotons L, Del Amo R, Llacuna S (2002) Bird community succession after fire in a dry Mediterranean shrubland. *Ardea* 90:303–310
- Herrando S, Brotons L, Llacuna S (2003) Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? *Ibis* 145:307–317
- Hirzel A, Guisan A (2002) Which is the optimal sampling strategy for habitat suitability modelling. *Ecol Modell* 157:331–341
- Hutto RL (1985) Habitat selection by nonbreeding, migratory land birds. In: Cody (ed) *Habitat selection in birds*. Academic Press Inc., p 455
- Le Houerou HN (1990) Agroforestry and sylvopastoralism to combat land degradation in the Mediterranean Basin: old approaches to new problems. *Agric Ecosyst Environ* 33(2):99–110
- Lloret F, Calvo E, Pons X, Diaz-Delgado R (2002) Wildfires and landscape patterns in the Eastern Iberian Peninsula. *Landsc Ecol* 17(8):745–759
- MacArthur RH, Wilson EO (1967) *The theory of island biogeography*. Princeton University Press, Princeton
- Masalles R, Vigo J (1987) La successió a les terres mediterrànies: sèries de vegetació. In: Terradas J (ed) *Ecosistemes Terrestres. La resposta als incendis i a d'altres pertorbacions*. Diputació de Barcelona, Barcelona, Spain
- Mayr E (1963) *Populations, species and evolution*. Academic Press, New York
- Mestre P, Peris S, Santos T, Suárez F, Soler B (1987) The decrease of Black-eared wheatear *Oenanthe hispanica* on the Iberian Peninsula. *Bird Study* 34:239–243
- Moreira F, Rego FC, Ferreira PG (2001) Temporal (1958–1995) pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. *Landsc Ecol* 16:557–567
- Murphy MT (2001) Source-sink dynamics of a declining Eastern Kingbird population and the value of sink habitats. *Conserv Biol* 15:737–748
- Norton MR, Hannon SJ, Schmiegelow FKA (2000) Fragments are not islands: patch vs landscape perspectives on songbirds presence and abundance in a harvested boreal forest. *Ecography* 23:209–223
- Oksanen J, Minchin PR (2002) Continuum theory revisited: what shape are species responses along ecological gradients? *Ecol Modell* 157(2–3):119–129
- Pérez B, Cruz A, Fernandez-Gonzalez F, Moreno JM (2003) Effects of the recent land-use history on the postfire vegetation of uplands in Central Spain. *Forest Ecol Manage* 182(1–3):273–283
- Piñol J, Terradas J, Lloret F (1998) Climate warming, wildfire hazard and wildfire occurrence in coastal Eastern Spain. *Clim Change* 38:345–357
- Pons P, Prodon R (1996) Short term temporal patterns in a Mediterranean shrubland bird community after wildfire. *Acta Oecol* 17:29–41
- Preiss E, Martin JL, Debussche M (1997) Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landsc Ecol* 12:51–61
- Prodon R, Fonts R, Athias-Binche F (1987) The impact of fire on animal communities in Mediterranean area. In: Traubald L (ed) *The role of fire on ecological systems*. SPB Academic Publ, The Hague
- Romme WH (1982) Fire and landscape diversity in subalpine forest of Yellowstone National Park. *Ecol Monogr* 52:199–221
- Rydgren K, Okland RH, Okland T (2003) Species response curves along environmental gradients. A case study from SE Norwegian swamp forests. *J Veg Sci* 14(6):869–880
- Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palaearctic migrant birds. *Biol Conserv* 131:93–105
- Scozzafava S, De Sanctis A (2006) Exploring the effects of land abandonment on habitat structures and on habitat suitability for three passerine species in a highland area of Central Italy. *Landsc Urban Plann* 75(1–2):23–33

- Sirami C, Brotons L, Martin JL (2007) Vegetation and songbird response to land abandonment: from landscape to census plot. *Divers Distrib* 13:42–52
- Sisk TD, Haddad NM, Ehlich PR (1997) Bird assemblages in patchy woodlands: modelling the effects of edge and matrix habitats. *Ecol Appl* 7(4):1170–1180
- Suárez-Seoane S, Osborne PE, Alonso JC (2002) Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. *J Appl Ecol* 39(5):755–771
- Tiainen J, Pakkala T (2001) Birds. In: Pitkänen M, Tiainen J (eds) Biodiversity in agricultural landscapes in Finland. Birdlife Finland Conservation Series, no. 3. Helsinki, Finland
- Viñas O, Baulies X (1995) 1:250 000 Land-use map of Catalonia (32,000 km²) using multitemporal Landsat-TM data. *Int J Remote Sens* 16(1):129–146
- Virkkala R, Luoto M, Rainio K (2004) Effects of landscape composition on farmland and red-listed birds in boreal agricultural-forest mosaics. *Ecography* 27(3):273–284
- Wiens JA (1994) Habitat fragmentation: island vs. landscape perspectives on bird conservation. *Ibis* 137:S97–S104
- Yee TW (2006) Constrained additive ordination. *Ecology* 87(1):203–213
- Zar JH (1998) *Biostatistical analysis*. Prentice-Hall, New Jersey