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Bird community specialization, bird conservation and disturbance: the role of wildfires

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Summary

1. Although niche theory predicts that disturbance should favour generalist species, the community-level implications of this pattern have been sparsely analysed. Here, we test the hypothesis that disturbance favours generalist species within communities, analysing effects of wildfires in bird communities in a Mediterranean climate area as a case study.
2. We use bird occurrence data in more than 500 1 × 1 km squares forming a gradient running from forest to completely burnt areas. The level of specialization of bird communities was estimated by means of three complementary species specialization indices, calculated for different landscape gradients and averaged at the community level (i.e. 1 × 1 km squares), and mean species rarity.
3. We also calculated mean habitat preferences along landscape gradients, as well as an index of conservation value and total species richness.
4. Different estimators of bird community specialization varied in contrasting fashion along the wildfire disturbance gradient, and thus we conclude that it is not justified to expect unique community responses to the sharp variations in habitat characteristics brought by wildfire disturbances.
5. Burnt areas tended to have rarer and urban-avoider bird species, whereas unburnt forests tended to have larger proportions of forest specialist species.
6. The mean conservation value of communities clearly increased towards the burnt extreme of the wildfire disturbance gradient, while this had a negligible effect on species richness.
7. Wildfires seem to play an important role for the maintenance of open-habitat, urban-avoider bird populations in Mediterranean landscapes and also to benefit a set of bird species of unfavourable European conservation status.
8. In this context, it cannot be unambiguously concluded that fire disturbance, even in a context in which fires are greatly favoured by human-related activities, leads to more functionally simplified communities dominated by generalist species.

Key-words: conservation value, Mediterranean landscapes, niche breadth, niche position, rarity

Introduction

Ecologists have devoted a great amount of work to analyse how ecological disturbances structure biological communities (Pickett & White 1985) and disturbance is nowadays generally recognized as essential for maintaining biodiversity (Hobbs & Huenneke 1992; Brawn, Robinson & Thompson 2001). Positive effects of disturbance on biodiversity have been recorded both at the local scale, with increases in α-diversity mainly through the prevention of competitive dominance, as well as at the regional scale, with disturbance generating environmental heterogeneity and thus enhancing β-diversity (e.g. Levin & Paine 1974; Townsend, Begon & Harper 2003).

Ecological theory predicts that the responses of particular organisms to disturbance should be related to their niche breadth (Futuyma & Moreno 1988). While specialist species would be favoured in more stable systems, abrupt environmental changes produced by disturbances would promote generalist species. However, the community-level implications of the relationships between disturbance and species' niche breadths have been sparsely analysed (Devictor *et al.*

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2008a; Devictor & Robert 2009). Disturbance-driven functional homogenization of communities, i.e. the substitution of unique or distinct functional roles played by specialists by others which are shared by many species (Olden & Rooney 2006), appears an especially relevant process in human-related disturbances, although exceptions to these common patterns have also been reported (e.g. Attum *et al.* 2006). Specialist organisms have been shown to be highly sensitive to human-induced habitat degradation, and thus they are suffering worldwide declines (Clavel, Julliard & Devictor in press). This ecological selectivity in population declines and extinctions is the main force driving functional homogenization.

Fires are important natural disturbances in many ecosystems (Brawn, Robinson & Thompson 2001; Backer, Jensen & McPherson 2004), although it is often doubtful how current fire regimes resemble the natural impact of this disturbance (Pausas & Keeley 2009). This is the case of many Mediterranean systems, where fire impact has grown enormously in the last decades, with strong effects on biodiversity patterns (Trabaud & Prodon 1993). If specialist species are to benefit from system stability, we expect fire disturbance, especially in case of disrupted fire regimes, to lead to generalist-dominated, functionally homogenized communities, as has been previously reported for other disturbances (Devictor *et al.* 2008a). However, fires are not alien disturbances in Mediterranean systems (Blondel & Aronson 1999; Pausas *et al.* 2008) and it is not clear that their impact may result in a clear-cut functional simplification of communities as in the cases of urbanization or habitat fragmentation.

In this work, we analyse the responses of different descriptors of bird communities to ecosystem disturbance to test the hypothesis that disturbance promotes generalist-dominated communities. Wildfires induce radical short-term modifications of habitat structure and resource availability that are followed by the much slower habitat changes of a secondary succession process. Consequently, post-fire bird communities are often dramatically different from those present in the pre-fire conditions, and it has been suggested, although not explicitly tested, that burnt areas could offer suitable conditions for habitat generalist species (Smucker, Hutto & Steele 2005). Differences in species composition between burnt and unburnt sites are often directional, since some traits, such as open-habitat preferences (e.g. Pons & Bas 2005), can be favoured in burnt areas. Some works have also suggested that the new habitats created by wildfires could be important for the persistence of threatened species (Moreira, Rego & Ferreira 2001; Pons & Bas 2005; Brotons, Herrando & Pons 2008). It would be therefore important to assess the community-level impacts of wildfires through integrative and ecologically meaningful community metrics (e.g. see Devictor *et al.* 2008a), to help monitoring biodiversity trends in a dynamic landscape scenario. Moreover, the importance of wildfires will probably increase in the future (Westerling *et al.* 2006), so patterns observed in the present situation could be a useful tool to anticipate biodiversity responses to fire regime modifications under global change.

To analyse community-level impacts of wildfires, we used data on bird species distribution from Catalonia, a Mediterranean region where a widespread, long-term forest expansion and maturation processes occur as a result of land abandonment and where wildfires are frequent (Gil-Tena, Brotons & Saura 2009; Vallecillo, Brotons & Thuiller 2009). Four measures of bird community specialization were calculated and their variation along a wildfire gradient composed of 551 1-km^2 squares and running from completely forested to completely burnt areas was analysed. Complementarily, the relationships between communities' habitat preferences (i.e. mean niche position) and the wildfire gradient were studied in order to better explain the changes in community specialization. Finally, species richness was recorded and an estimate of the conservation value of bird communities was calculated to analyse their variation along the wildfire disturbance gradient. Thus, we intend to give a general picture of the large-scale, community-level effects of wildfire disturbances.

Materials and methods

STUDY AREA AND BIRD DATA

This study was conducted in Catalonia (NE Iberian Peninsula), a region of some 32 000 km^2 that comprises a wide environmental heterogeneity, from coastal habitats to high altitude mountain ranges (up to 3143 m above sea level) (Fig. 1), and has a Mediterranean climate throughout most of its area. Recent land abandonment in the

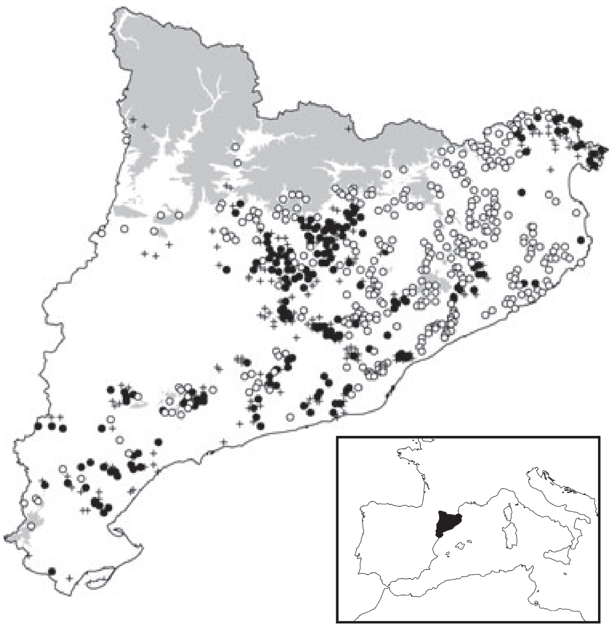

Fig. 1. Maps of the study area (Catalonia, north-eastern Iberian Peninsula) showing the location of the 1 × 1 km squares selected to define the wildfire disturbance gradient (FIRE). Black dots represent squares in which wildfires (of any extent) had occurred in the period 1986–99, while empty dots represent unburned squares. Crosses mark 1 × 1 km squares in which wildfires had taken place between 1986 and 1999, but did not meet the criteria to be included in the analyses. Shadowed zones denote areas above 1000 m.

European part of the Mediterranean basin has led to a progressive woody plant encroachment and to a higher extent of the area affected by wildfires (Blondel & Aronson 1999). In the particular case of Catalonia, shrubland and forest cover have remained relatively constant over the last decades, even though many areas have changed from shrubland to forest and vice versa, due to a dynamic equilibrium between forest succession and wildfires (Vallecillo, Brotons & Thuiller 2009).

Data on the occurrence of diurnal birds were taken from the Catalan Breeding Bird Atlas (Estrada *et al*. 2004). Within each UTM, 100 km^2 square in Catalonia from 5 to 10 1 km^2 squares were selected in a stratified fashion in order to cover as much as possible of the environmental variability present in the area. Two 1-h bird surveys were performed in each 1 km^2 between March and July from 1999 to 2002, and the occurrence (presence/absence) of bird species was recorded. Aquatic bird species and those strictly depending on water bodies to breed were excluded from the data set (Julliard *et al*. 2006). Specific composition of breeding bird communities was finally recorded for 3076 1 km^2 squares.

DEFINITION OF THE WILDFIRE DISTURBANCE GRADIENT

Each surveyed square was characterized by its forest cover (in %, from the 1997 Catalan land use map) and the percentage of the total area burnt by wildfires from 1986 to 1999 (from fire perimeters provided by the Catalan government, available at http://mediambient.gencat.net/cat/inici.jsp). Squares in which the sum of forest percentage cover and percentage of burnt area was equal or larger than 75% were selected to create a fire to forest gradient (FIRE). Values taken by the FIRE gradient were obtained by subtracting the % forest cover to the % total burnt area within the square. Thus, FIRE ranges between −100 and 100, running from totally afforested unburnt areas to totally burnt ones. Along this gradient, disturbance is quantified in terms of its size (i.e. burnt area), a main characteristic of ecological disturbances (Pickett & White 1985). The FIRE gradient included exclusively squares at altitudes under 1000 m a.s.l., as wildfires hardly ever occur at higher altitudes. Squares in which < 15 breeding bird species had been recorded ($N = 24$) were not considered in the analyses, since they were assumed to be poorly surveyed. The final disturbance gradient comprised 551 1-km^2 squares out of which 202 (36·7%) had been burnt by wildfires, whether totally or partially, in the 1986–99 period (Fig. 1).

DEFINITION OF RESPONSE VARIABLES

Bird communities, defined hereafter as the set of species that occur in a given 1-km^2 square, were described according to three groups of variables: (i) specialization level (three variables quantifying average degree of specialization in relation to different landscape gradients plus average rarity); (ii) niche position (three variables related to the average preferences for landscape gradients' extremes) and (iii) mean conservation status and total species richness (Table 1).

Community specialization estimates derive from species specialization indices created for 103 terrestrial bird species on the basis of the variation of their frequency of occurrence in over 2800 1-km^2 squares distributed along landscape gradients in Catalonia, as thoughtfully described in Clavero & Brotons (2010). In short, three orthogonal landscape gradients issued from the first three axes of a Principal Component Analysis were used as niche dimensions and divided into segments. These gradients of variation in landscape characteristics were interpreted, based on the weights of original variables as: (i) a bioclimatic gradient (ranging from more Mediterranean to more temperate conditions); (ii) an urban gradient (ranging from urban areas to those with few urban uses, mainly characterized by Mediterranean shrub cover) and (iii) a structural gradient (ranging from open landscapes to forests). The coefficients of variation (CV) of species frequencies of occurrence along gradient segments were used as a measure of bird species specialization. Final species specialization values were the standardized residuals of the regression of CV values against total occurrences (both variables were strongly related). According to Devictor *et al*. (2010), our specialization measures represent a Grinnellian approach to the realized niche breadths of bird species (in fact, their inverses) in relation to landscape characteristics, in which we quantify the actual breadth of species' requirements. It should be noted that, although specialization indices and the FIRE gradient derive from the same data set, we do not expect any intrinsic link between those variables. This is because any given niche breadth (i.e. a certain value of species' specialization) could be found at any position of the gradient. For example, a specialist (narrow niche) along a certain gradient could show preferences for any of the two gradient extremes or for intermediate gradient positions.

As specialization measures described above were independent from the frequencies of occurrence of species, rarity was used as an additional estimator of specialization, relying on the assumption that widespread, common species are usually generalists while specialist

Table 1. Summary of the descriptors of bird communities used as response variables in this study

Index type	Code	Description
Specialization	BIOCL Bioclimatic gradient	Mean specialization of bird communities along a bioclimatic gradient
	URBAN Urban gradient	Mean specialization of bird communities along an urban gradient
	STRUC Structural gradient	Mean specialization of bird communities along a farmland to forest gradient
	RARITY	Average rarity of bird species in Catalonia
Niche position	pref-BIOCL	Mean habitat preference along a bioclimatic gradient. Low values: hot-dwelling communities; high values: cold-dwelling communities
	pref-URBAN	Mean habitat preference along an urban gradient. Low values: urban communities; high values: urban-avoider communities
	pref-STRUC	Mean habitat preference along a structural gradient. Low values: farmland communities; high values: forest communities
Conservation	Conservation value	Mean species' scores based on their European conservation status (SPEC)
	Richness	Total species richness

species tend to be rare (e.g. Hurlbert & White 2007). Regional rarity was calculated for Catalonia subtracting to 1 the proportion of squares in which the species was present (i.e. if a species was present in all squares, rarity would equal 0). Finally, four indices of bird community specialization were obtained by averaging the values of bird species occurring in 1 km^2 squares: BIOCL (related to the bioclimatic gradient), URBAN (related to the urban gradient), STRUC (related to the structural gradient) and RARITY (mean rarity). High values of any of these indices indicate a high level of community specialization (i.e. narrow average niches) in relation to a particular landscape gradient.

Species' niche positions in relation to the same three landscape gradients were estimated through their preference for any of the gradients' extremes, using the slope of the relationship between the frequency of occurrence of each bird species and landscape gradients (Clavero & Brotons 2010). When averaged for communities, these estimators of niche position produced three indices, which were coded as pref-BIOCL, pref-URBAN and pref-STRUC. Negative values of any of these indices denote an average preference for the negative end of the particular gradient, whereas positive values denote preference for the positive one, preferences being higher for larger absolute values (see Table 1).

The conservation value of bird communities was assessed through an adaptation of the index used by Pons *et al*. (2003), which takes into account each species' European conservation status (SPEC; BirdLife International 2004). A SPEC value, in geometric progression of increasing conservation concern, was assigned to each species as follows: Non-SPEC = 1; Non-$SPEC^E$ = 2; SPEC 3 = 4; SPEC 2 = 8 (there were no SPEC 1 species among the 551 squares selected to construct the wildfire gradient). Thus, these weights give twice the conservation value to a species in a certain SPEC level to that of any species in the immediate lower SPEC level. Species' values were then averaged to obtain the community conservation value. Finally, total species richness for every 1 km^2 square was also recorded.

DATA ANALYSES

The relationships between the nine response variables shown in Table 1 and the disturbance gradient (FIRE) were studied through multiple regression analyses. Altitude and species richness were used as additional independent variables, as they could influence bird community patterns. Indeed, Clavero & Brotons (2010) showed that species richness was negatively related to most estimators of community specialization, while being positively related to mean rarity. Altitude can also be expected to influence average niche properties as well as other community descriptors, due to the close relationships existing between altitude and the distributions of many species (Estrada *et al*. 2004). The squared value of FIRE was also included in the analyses in order to allow the identification of unimodal responses of communities to the disturbance gradient. For sake of simplicity and comparability of results no model selection procedure was used, and complete multiple regression models (i.e. four independent variables) were fitted in all cases. To reduce the probability of committing type-I errors due to multiple testing, the significance threshold was set at a conservative $P < 0{\cdot}001$. The strength of the associations between response variables and each individual predictor was assessed through the examination partial Eta squared [$\eta_p^2 = SS_{effect}/(SS_{effect} + SS_{error})$]. As R^2, η_p^2 is a dimensionless measure of effect size that is independent of the degrees of freedom used in the analyses (Tabachnick & Fidell 2001).

There were large parts of our study area in which wildfires were rare or inexistent (see Fig. 1), a fact that could influence our results. To ensure the robustness of the observed patterns the analyses described above were applied to two nested data sets. A first approach included the 551 1 km^2 squares that had been selected for the disturbance gradient. The second approach used exclusively squares that had burnt between 1986 and 1999 (n = 202), thus ensuring that the analyses were not including areas where wildfire occurrence is highly improbable (see Fig. 1). Results using both data sets were very similar and thus we present only statistics corresponding to the whole data set. However, burnt and unburnt squares are always identified in the graphics.

Results

FIRE disturbance gradient had significant linear effects on all four response variables dealing with bird community specialization. However the responses of the different specialization indicators were heterogeneous, and thus it was not possible to reject or accept in a general manner our initial hypothesis that disturbance promotes more generalist communities (Table 2).

Once the effects of altitude and species richness had been taken into account, BIOCL showed a linear, although rather weak ($\eta_p^2 = 0{\cdot}05$), increase along FIRE (Fig. 2). The response of URBAN to the disturbance gradient followed a similar, though stronger pattern, with more specialized communities towards the most intensely disturbed end of FIRE. Burnt areas also bore bird communities composed on average of rarer species than undisturbed, afforested ones (Table 2). There was also a significant, positive quadratic effect of FIRE on RARITY (i.e. concave relationship)

Table 2. Results of the multiple regression models analysing the variation in different indices of the level of specialization of bird communities (see Table 1), indicating the direction of significant relationships (negative or positive slopes), statistical significance of effects (those with $P < 0{\cdot}001$ are marked in bold) and effect sizes (measured as partial Eta squared η_p^2). Independent variables are altitude (meters above sea level), species richness, the wildfire gradient (FIRE) and the gradient's squared values ($FIRE^2$). Coefficients of determination (R^2), F-values and significance levels for models are also given in the left column

		Slope	Significance	η_p^2
BIOCL	Altitude	(−)	**< 0·001**	**0·10**
$R^2 = 0{\cdot}15$	Richness		0·03	0·01
$F_{4,546} = 24{\cdot}1$	FIRE	(+)	**< 0·001**	**0·05**
$P < 0{\cdot}001$	$FIRE^2$		0·22	< 0·01
URBAN	Altitude	(−)	**< 0·001**	**0·02**
$R^2 = 0{\cdot}24$	Richness	(−)	**< 0·001**	**0·05**
$F_{4,546} = 42{\cdot}4$	FIRE	(+)	**< 0·001**	**0·19**
$P < 0{\cdot}001$	$FIRE^2$		0·96	< 0·01
STRUC	Altitude	(+)	**< 0·001**	**0·05**
$R^2 = 0{\cdot}28$	Richness	(−)	**< 0·001**	**0·03**
$F_{4,546} = 52{\cdot}3$	FIRE	(−)	**< 0·001**	**0·19**
$P < 0{\cdot}001$	$FIRE^2$		0·23	< 0·01
RARITY	Altitude	(+)	**< 0·001**	**0·11**
$R^2 = 0{\cdot}46$	Richness	(+)	**< 0·001**	**0·23**
$F_{4,546} = 115{\cdot}2$	FIRE	(+)	**< 0·001**	**0·27**
$P < 0{\cdot}001$	$FIRE^2$	(+)	**< 0·001**	**0·04**

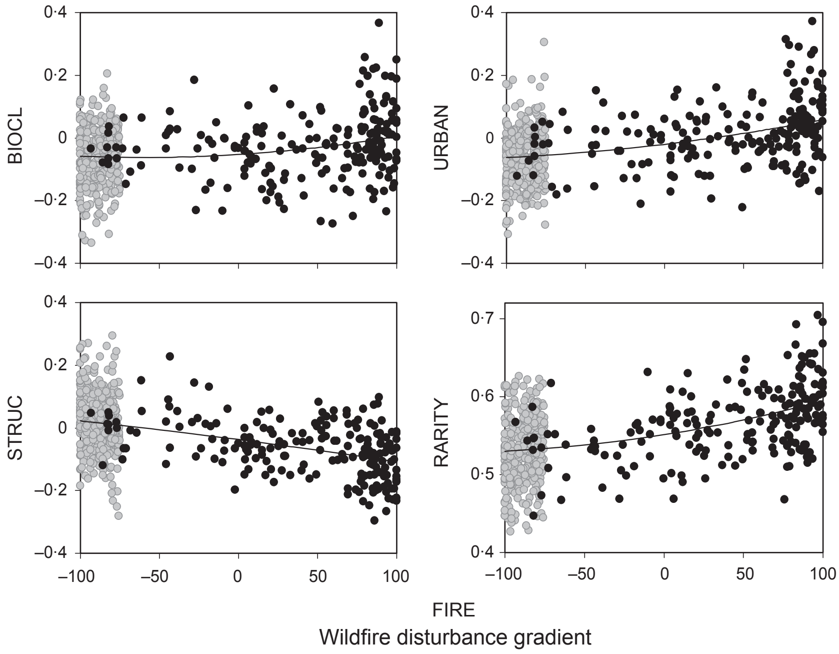

Fig. 2. Relationships between the wildfire disturbance gradient (FIRE) and indices of bird community specialization (see Table 1 for code definition) for 551 1 km^2 squares in Catalonia (NE Iberian Peninsula). FIRE gradient runs from unburnt squares totally covered by forest to unforested squares that have burnt completely between 1986 and 1999. Black dots represent squares in which wildfires (of any extent) had occurred in the period 1986–99, while grey dots represent unburned squares. Shown fits are quadratic polynomial regression lines in all cases.

although that of the linear component of the relationship was almost seven times stronger (see η_p^2 values in Table 2). On the other hand, forest areas bore more specialized bird communities in terms of species' use of the farmland–forest gradient (STRUC). Thus, while three community specialization indicators (URBAN, RARITY and, to a lesser degree, BIOCL) reported negative relationships between average niche breadth and ecological disturbance, the fourth one (STRUC) followed the contrary pattern, with more specialized communities occupying undisturbed areas (Fig. 2).

Average niche position of communities responded much strongly to FIRE than indices of community specialization (compare R^2 values in Tables 2 and 3). Bird communities at the forested end of FIRE included on average colder-dwelling species (i.e. higher pref-BIOCL) and, as obviously expected, species with stronger preferences for forest habitats (higher pref-STRUC). On the other hand, bird communities in forest areas had a more urban-dwelling character than those occupying areas affected by wildfires (Fig. 3).

Bird communities in burnt areas included, on average, species of higher European conservation concern than those using undisturbed afforested areas (Table 3). Wildfire disturbance thus positively influenced the presence of bird species with both unfavourable conservation status and restricted geographical distribution (Figs 2 and 4). The relationship between species richness and FIRE was rather weak (see R^2 values in Table 3), with a significant negative quadratic effect of FIRE denoting higher species richness at intermediate gradient positions.

Table 3. Results of the multiple regression models analysing the variation in different indices of community niche position (see Table 1), conservation value and species richness, indicating the direction of the significant relationships (negative or positive slopes), statistical significance of effects (those with $P < 0{\cdot}001$ are marked in bold) and effect sizes (measured as partial Eta squared η_p^2). Independent variable codes as in Table 2. Coefficients of determination (R^2), F-values and significance levels for models are also given in the left column

		Slope	Significance	ηp^2
Niche position variables				
pref-BIOCL	Altitude	(+)	**< 0·001**	**0·47**
$R^2 = 0{\cdot}68$	Richness		0·10	< 0·01
$F_{4,546} = 290{\cdot}7$	FIRE	(–)	**< 0·001**	**0·48**
$P < 0{\cdot}001$	FIRE^2		0·53	< 0·01
pref-URBAN	Altitude	(+)	**< 0·001**	**0·21**
$R^2 = 0{\cdot}44$	Richness		0·67	< 0·01
$F_{4,546} = 106{\cdot}1$	FIRE	(+)	**< 0·001**	**0·36**
$P < 0{\cdot}001$	FIRE^2		0·002	0·02
pref-STRUC	Altitude	(+)	**< 0·001**	**0·24**
$R^2 = 0{\cdot}60$	Richness	(–)	**< 0·001**	**0·06**
$F_{4,546} = 207{\cdot}7$	FIRE	(–)	**< 0·001**	**0·47**
$P < 0{\cdot}001$	FIRE^2		0·56	< 0·01
Conservation-related variables				
Conservation value	Altitude		0·18	< 0·01
$R^2 = 0{\cdot}53$	Richness		0·02	0·01
$F_{4,546} = 151{\cdot}4$	FIRE	(+)	**< 0·001**	**0·49**
$P < 0{\cdot}001$	FIRE^2		0·09	0·01
Richness	Altitude		0·94	< 0·01
$R^2 = 0{\cdot}07$	FIRE		0·01	0·01
$F_{4,547} = 13{\cdot}7$	FIRE^2	(–)	**< 0·001**	**0·04**
$P < 0{\cdot}001$				

Discussion

Niche evolution theory predicts that narrow niches should be favoured in stable environments, while generalist species could be able to thrive in heterogeneous environments, whether in time or in space (Futuyma & Moreno 1988). Disturbance leads to sharp temporal discontinuities in habitat characteristics and resource availability, and both theoretical and empirical works have related it with the

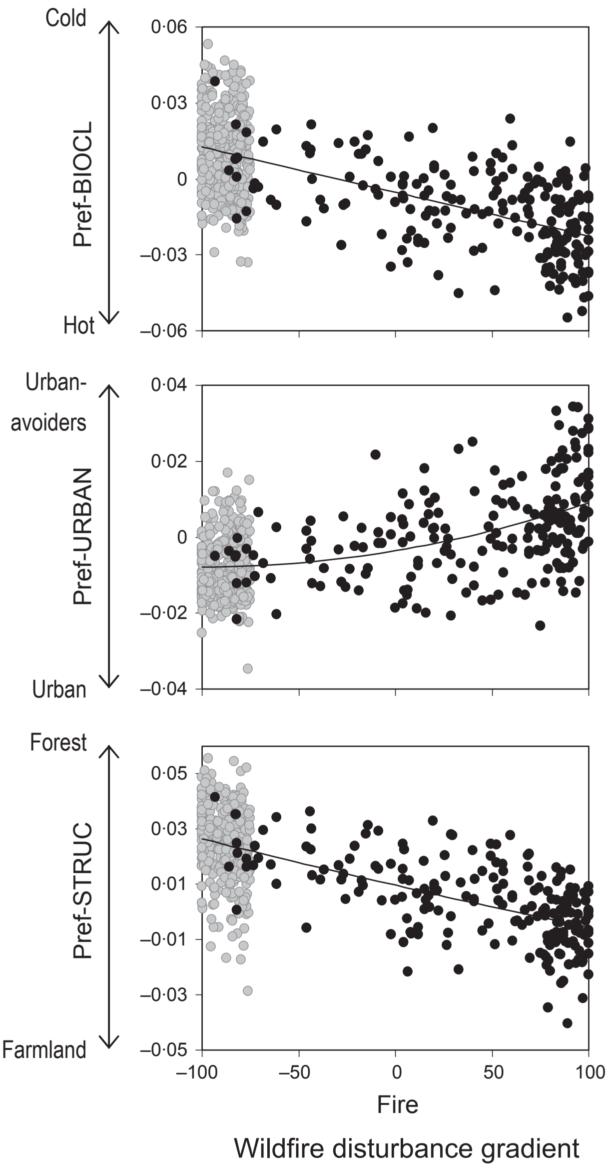

Fig. 3. Relationships between the FIRE gradient and indices of bird community average niche position (see Table 1 for code definition) for 551 1 km^2 squares in Catalonia (NE Iberian Peninsula). As in Fig. 2, black dots represent burned squares and grey dots represent unburned ones. Shown fits are quadratic polynomial regression lines in all cases.

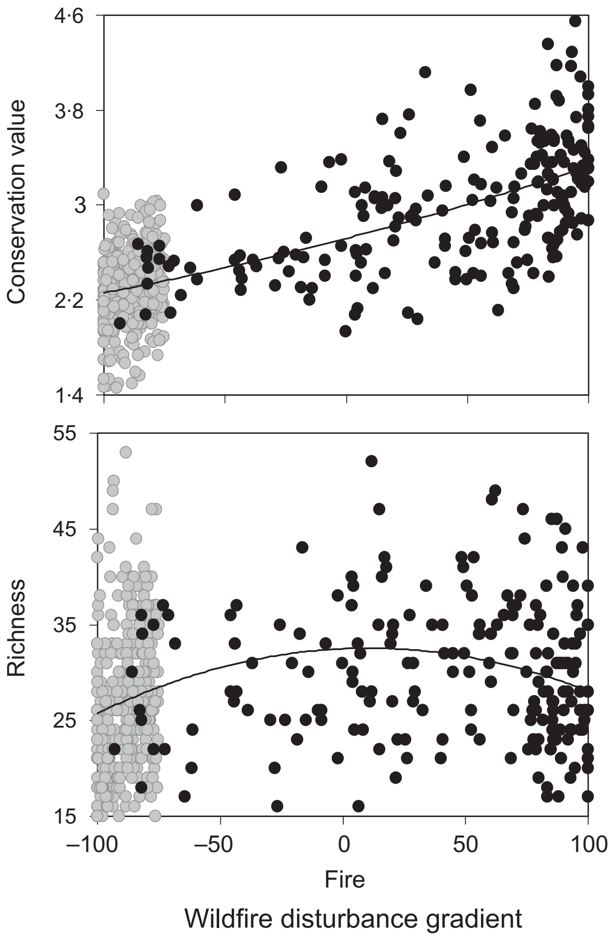

Fig. 4. Relationships between the FIRE gradient and conservation-related variables of bird community for 551 1 km^2 squares in Catalonia (NE Iberian Peninsula). As in Fig. 2, black dots represent burned squares and grey dots represent unburned ones. Shown fits are quadratic polynomial regression lines in all cases.

substitution of specialist species by generalist ones (Marvier, Kareiva & Neubert 2004; Devictor *et al.* 2008b). Wildfires are typical examples of disturbance events, giving raise to rapid and profound changes in habitat structure, followed by a slower, although constant, dynamic process of secondary succession. It could be thus predicted that specialist species would be negatively affected by such disturbances and that burned areas would be occupied by generalist species, leading to a decrease of the level of specialization of communities after wildfire occurrence. However, relationships between wildfire disturbance and the level of specialization of bird communities in Catalonia often did not match those predictions. Although wildfire led to more generalist bird communities in terms of their use of the structural gradient, other community specialization indices tended to increase after fire.

Our multidimensional approach to estimate the specialization level could explain some apparent contradictions between some of our results and both theorized and reported relationships between specialization and disturbance. Previous works dealing with the level specialization of bird communities did not take into account niche multidimensionality, estimating the positions of species or communities along a unique specialist–generalist gradient (e.g. Julliard *et al.* 2006; Devictor *et al.* 2008a). However, as each particular species can be a specialist along a given niche dimension while being generalist along another, the level of specialization of communities along different niche dimensions can also respond differently and with variable strength to a particular type of disturbance. In our results, these ambiguous patterns arose along the wildfire disturbance gradients (Fig. 2). Clavero & Brotons (2010) also found heterogeneous responses of different community specialization indices to an agricultural–forest gradient, and suggested that the combined analyses of specialization and associated niche position estimators could clarify seemingly confounding patterns.

Other works had previously reported responses to disturbance of specialist and generalist organisms that depart from the general predictions of the niche theory. For example, Attum *et al.* (2006) showed that sand-dune specialist lizards were able to survive in degraded and human-perturbed sites, from where more generalist species tended to disappear, and related these patterns to the increased environmental harshness of disturbed sites. As in this case, context-dependent effects of fire-induced disturbances on Mediterranean landscapes, discussed below, can explain the observed positive relationships between the degree of specialization and ecological disturbances. In fact, the particular characteristics of each type of disturbance can arguably have specific consequences on the responses of communities, which can be mediated by the landscape context. To analyse the effects of disturbance on bird communities in France, Devictor *et al.* (2008a) defined disturbance as the rate of habitat turnover in a 10-year period. Thus, any change in habitat characteristics would count equally in the final quantification of disturbance, independently of the habitat types involved. For example, two areas would have been perceived as equally disturbed if one had changed from shrub to forest due to secondary succession and the other had passed from forest to shrub due to the effects of wildfire. Obviously, the responses of bird communities to these two habitat changes would be different, if not opposite. The use of meaningful disturbance gradients should allow a more comprehensive approach to analyse the dynamics of community characteristics and to relate these changes to specific population processes.

Fire is a fundamental disturbance agent in many systems, being especially important in Mediterranean-climate environments due to the combination of hot and dry summers with dense vegetation/fuel structure (Moreno & Oechel 1994). Landscape mosaics in the Mediterranean Basin are to a great extent the result of a millenary human intervention, with forest clearance (related to cattle grazing, agriculture and associated fires) having led to a heterogeneous matrix of open areas, shrublands and forests (Thompson 2005). In the European part of the Mediterranean basin, the depopulation of rural areas and the resulting land abandonment during the 20th century has favoured a widespread forest expansion and the maturation of previously established forest masses (Gil-Tena, Brotons & Saura 2009). In this context, wildfires are increasingly becoming a human-related disturbance and practically the most important force creating and maintaining open habitats (Preiss, Martin & Debussche 1997; Moreira, Rego & Ferreira 2001), thus being a critical factor determining the distribution of many open-habitat and shrub-dwelling bird species (Brotons, Pons & Herrando 2005; Brotons, Herrando & Pons 2008; Vallecillo, Brotons & Thuiller 2009). The dynamics of bird community composition in burnt areas are in most cases closely linked to the time passed after fire (Jacquet & Prodon 2009) and it would be therefore interesting to analyse the temporal changes in the average level of specialization of bird communities following fire occurrence. Our data set, however, was not specifically designed to this aim and thus we focussed in the spatial patterns in bird communities generated by fire disturbance.

Bird communities within the Mediterranean basin often reach their maximum diversity in agro-sylvo-pastoral landscape mosaics (Farina 1997), while forest areas host impoverished communities mainly composed of generalist forest species, most of which had evolved outside the Mediterranean region (Covas & Blondel 1998; Suarez-Seoane, Osborne & Baudry 2002). In this sense, Clavero & Brotons (2010) showed that bird communities in agricultural areas had on average rarer species and were often more specialized than those in forests, and concluded that secondary afforestation process due to land abandonment was promoting the functional homogenization of bird communities. Similar patterns emerged often in the present results when confronting community specialization measures with the wildfire disturbance gradient. Wildfires generate new available habitats for open-habitat and shrubland birds (Pons & Bas 2005) many of which disappear in the middle or long term following fire (Preiss, Martin & Debussche 1997; Jacquet & Prodon 2009; Pons & Clavero 2010), progressively leading to bird communities characterized by forest generalist and common species. The fact that forest bird communities were on average more urban-dwelling that those occupying burnt areas could rely in the facility with which many forest birds occupy urban environments (e.g. Croci, Butet & Clergeau 2008). Arguably, forest birds are able to find appropriate habitats in urban areas, while the majority open-habitat and shrubland species are unable to colonize such environments.

On the other hand, the average level of specialization of bird communities along the structural gradient (STRUC) was higher towards the forest end of the wildfire disturbance gradient, a pattern that was related to the expected dominance of species with clear forest habitat preferences (see pref-STRUC patterns, Fig. 3). Burnt areas are often complex mosaics of habitats formed because the impact of fire and the vegetation recovery process are subjected to spatial variations due to orography, soil structure or other features as well as by the presence of different structures (partially burnt and/or dead trees and shrubs) that remain after fire (e.g. Herrando, Brotons & Llacuna 2003). These habitats mosaics can be occupied by heterogeneous bird communities, including open-habitat specialists, shrubland, edge habitats and even some forest bird species (Brotons, Herrando & Martin 2004; Pons & Bas 2005; Jacquet & Prodon 2009), while only the latter form the bulk of forest communities.

Bird communities occupying burnt areas had on average higher conservation value than those from unburned forests. Brotons, Herrando & Pons (2008) showed that wildfires were providing adequate habitat for the ortolan bunting (*Emberiza hortulana*), a species of European conservation concern. Here we show that particular population processes related to the occupation of burnt areas, like that of the ortolan bunting, result in a clear increase in the average conservation value of species occupying burnt sites. Again, this pattern should be related with the role of wildfires in the creation of open habitats, which could be colonized by farmland and shrub-dwelling bird species. Across Europe these farmland species have often suffered strong declines and have an unfavourable conservation status, a situation that contrasts with the generalized favourable trend of forest birds (e.g. Gregory *et al.* 2005).

Interestingly, while most average characteristics of bird species sharply varied along the wildfire disturbance gradient, species turnover did not result in any clear change in total richness. The unimodal response of species richness to the wildfire disturbance gradient could be interpreted as a support for the intermediate disturbance hypothesis, according to which higher diversity levels would be attained at intermediate disturbance levels. However, we think that effect sizes (i.e. η_p^2) are too small to extract strong conclusions on the patterns in species richness. In a local-scale, long-term wildfire succession study in southern France, Jacquet & Prodon (2009) neither found clear trends in overall bird species richness in spite of a clear temporal species turnover process closely associated to their position along an open-habitat to forest gradient. Thus, we agree with Devictor *et al.* (2008a) in that metrics that have been traditionally used to assess community responses to disturbance, such as richness and diversity, could be unable to accurately reflect the impacts of disturbances and that the characteristics of species involved in community changes should be taken into account.

The patterns described here imply that wildfires may be positive for the conservation of Mediterranean avifauna, as burnt areas are most often occupied by more specialized, rarer and more threatened bird communities than forests. As explained above, this is due to the role of wildfires as the main force maintaining current landscape heterogeneity in an area where socio-economic drift has promoted the abandonment of marginal agricultural areas and the subsequent expansion and maturation of forests (e.g. Preiss, Martin & Debussche 1997). Landscape heterogeneity may be also maintained through alternative management means, such as the promotion of agriculture and grazing in marginal areas or by applying controlled prescribed burnings (Sirami *et al.* 2010). These measures may contribute to hamper the negative economic and human damages that wildfires may cause and to reduce the impacts of very large fires (e.g. by reducing fuel availability and breaking the continuity of forest masses). However, such management practices imply very profound changes in the attitude of managers and the public opinion, who most often see forests as the paradigm of nature conservation and fires as environmental catastrophes (Gomez-Limon & de Lucio Fernandez 1999; Pausas *et al.* 2008).

Conclusions

Our results show that different estimators of bird community specialization varied in contrasting fashion along the wildfire disturbance gradient and thus we conclude that it may not be justified to expect unique community responses to the sharp variations in habitat characteristics brought by disturbances. The variability in the relationships between the level of specialization of communities and disturbance respond to the different ways in which specialization is quantified and to the specific nature of the disturbance analysed. Regarding the specific focus of our work, we cannot unambiguously conclude that fire disturbance, even in a context in which fires are greatly favoured by human-related activities, leads to functionally simplified communities dominated by generalist species.

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