RESEARCH PAPER

Functional homogenization of bird communities along habitat gradients: accounting for niche multidimensionality

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ABSTRACT

Aim To test whether functional homogenization of bird communities is promoted by anthropogenic landscape transformation, using specialization and habitat preference indices that account for the multidimensionality of niches.

Location Catalonia, north-east Iberian Peninsula.

Methods We used data on bird species occurrences and landscape features in 2834 1-km^2 squares. Three orthogonal landscape gradients, which were taken as niche dimensions, were defined by means of principal components analysis (PCA). Specialization and habitat preference indices were created for 103 terrestrial bird species on the basis of their frequency of occurrence variation along the landscape gradients. These indices, together with species rarity, were then averaged for bird communities. We then analysed the patterns of variation of communities' mean specialization, mean rarity and mean habitat preference values along a gradient of agricultural–forest habitat mosaics.

Results Wherever we found a significant variation in the degree of specialization along the agricultural–forest gradient, agricultural habitats held more specialized bird communities than did forest ones and bore, on average, rarer species. Thus, results contradicted our initial hypothesis that humanized areas would bear more functionally homogenized bird communities. Higher α-diversity values tended to be associated with generalist communities and with those having rarer species.

Main conclusions Estimations of bird community specialization for different niche dimensions can behave differently along certain landscape gradients, and some of these differences can be explained by the variation of mean habitat preferences. Thus, we argue that a multidimensional approach to assess average niche breadth of communities can be more informative than a unidimensional measure. Our results suggest that widespread land abandonment and current secondary forest expansion throughout the Mediterranean area are promoting functional homogenization of bird communities. It would be desirable to construct larger-scale indicators of functional homogenization in order to monitor communities' responses to widespread landscape changes.

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INTRODUCTION

Human activities are driving a world-wide process of loss of biodiversity (Vitousek *et al.*, 1997; Olson *et al.*, 2002). Species extinctions are one of the faces of this process, but human impacts are also producing profound changes in the structure of communities, many of which are related to processes of biotic homogenization (McKinney & Lockwood, 1999; Olden *et al.*,

2004). These changes are crucial, as it is the composition and structure of communities, and not species richness, that defines the role of biodiversity in ecosystem functioning (Kinzig *et al.*, 2002). Biotic homogenization is a multifaceted concept that refers to the processes by which biotas lose their biological distinctiveness at any level of organization, whether genetic, taxonomic or functional (Olden & Rooney, 2006). Functional homogenization occurs whenever there is a reduction in the functional diversity of communities, a process related to the substitution of unique or distinct functional roles within ecosystems by others that are shared by many species, leading to high levels of functional redundancy (Olden & Rooney, 2006). Functional homogenization is thus promoted by the local proneness to extinction of specialist organisms, a pattern that has been stressed in many previous studies (e.g. Foufopoulos & Ives, 1999; Owens & Bennet, 2000).

In contrast to the patterns in taxonomic homogenization and the mechanisms creating them, which have been analysed in different regions and for a variety of organisms, few works have quantitatively studied functional homogenization (Olden & Rooney, 2006). Its analysis is often hindered by the way specialization is defined. Species are often classified either as specialist or generalist based on the use of a certain resource (e.g. Attum *et al.*, 2006), even though they should be placed along continuous gradients going from specialization to generalism. In a recent work, Julliard *et al.* (2006) developed a continuous index of specialization for bird species based on the coefficient of variation of their densities among habitat classes. These indices, averaged for local communities, were later used to explicitly relate functional homogenization to urbanization (Devictor *et al.*, 2007) and landscape disturbance and fragmentation (Devictor *et al.*, 2008a).

The specific specialization index designed by Julliard *et al.* (2006) has, however, the shortcoming of being calculated using categorical habitat divisions, despite the fact that habitats are not discrete and could be ordered along continuous gradients. A categorical habitat approach fails to relate the variation in species presences or densities to the similarity of habitat types under analysis. Thus, although species can be classified along specialization gradients, the direction of their possible habitat preferences (i.e. their niche position) cannot be numerically assessed. Moreover, a single measure of specialization probably does not to take into account the multidimensionality of the species niches and it could overlook the fact that a species can be highly specialized along one habitat gradient while acting as a generalist along others.

In this work we propose a methodology to calculate species indices of specialization at the landscape scale based on that of Julliard *et al.* (2006), though modified to incorporate the continuous variation of landscape characteristics and the unavoidable multidimensional nature of species niches. We employed multivariate statistics to create orthogonal landscape gradients, which were interpreted as niche dimensions. We then calculated community specialization indices for each niche dimension and analysed the patterns of variation of those indices along an agricultural–forest landscape gradient. The possible role of agricultural land uses on functional homogenization of communities has not yet been analysed, even though agriculture is one of the most widespread human impacts in terms of frequency and land occupancy. Previous works have shown that functional homogenization of bird communities (i.e. a trend towards generalist-dominated communities) is promoted both by urbanization and habitat disturbance and fragmentation (Devictor *et al.*, 2007; Devictor *et al.*, 2008a). On the other hand, Smart *et al.* (2006) related both spatial and temporal increases in functional similarity among plant communities to reductions in species richness. Therefore, we also took into account local species richness when analysing the variation in the community specialization indices.

MATERIALS AND METHODS

Bird and environmental data

This study was carried out in Catalonia, a 31,930 km^2 territory located in the north-east Iberian Peninsula. The area features a high environmental diversity that is mainly related to altitude, ranging from sea level to 3143 m a.s.l. Climate is typically Mediterranean throughout most of Catalonia, although more temperate climatic conditions with attenuated summer droughts are also present, usually associated with mountain ranges.

Data on diurnal bird occurrences were obtained from the Catalan Breeding Birds Atlas (Estrada *et al.*, 2004), which reports information on bird distribution in Catalonia between 1999 and 2002. During that period, 10 1-km^2 squares were surveyed in each of the 100-km^2 Universal Transverse Mercator (UTM) squares included in the study area, thus covering most of its environmental variation. The final dataset included 3077 1-km^2 squares. In each of these squares, two 1-h bird surveys were performed between March and July, and the presence/absence of bird species was recorded. We excluded from our analyses aquatic birds, including reed-breeding species and those strongly depending on water bodies to breed, as they might not be correctly surveyed with the field methodology employed (e.g. Julliard *et al.*, 2006) and their habitat preferences could be independent of landscape features used in this work. From the complete dataset, we excluded those squares with altitudes lower than 20 m and higher than 2000 m, resulting in a final pool of 2834 squares.

Landscape characteristics of the 1-km^2 squares were defined by 16 variables, including percentage cover of 11 landcover categories, three climatic and orographic variables and two variables related to the proximity of human uses (Table 1).

Indices of specialization of bird species

We calculated independent specialization measures for the different landscape gradients, and thus did not assume that a species should always behave as either a specialist or generalist along different niche dimensions. To summarize landscape-scale environmental variation, we applied a principal components analysis (PCA) to a matrix of 2834 rows (1-km^2 squares) and 16

Table 1 Factor loadings and eigenvalues resulting from the principal components analysis (PCA) applied to a matrix of 2834 1-km^2 squares × 16 landscape variables.

Variable	PC1	PC2	PC3
Land uses			
Sclerophyllous forests	−0.03	−0.26	**0.45**
Coniferous forests	0.07	0.16	**0.58**
Deciduous forests	**0.54**	−0.04	0.04
Mediterranean shrub	−0.39	0.32	0.23
Montane shrub	**0.48**	0.13	−0.07
Meadows	**0.52**	0.08	−0.08
Ligneous dry farming	**−0.45**	0.21	−0.09
Herbaceous dry farming	0.02	−0.04	**−0.52**
Irrigation lands	−0.14	−0.07	**−0.54**
Urban	−0.04	**−0.60**	−0.14
Suburban	−0.07	**−0.56**	0.19
Climatic-orographic			
Altitude	**0.83**	0.33	0.27
Annual rainfall ($\log_{10}X$)	**0.71**	−0.11	**0.53**
Mean annual temperature	**−0.87**	−0.30	−0.25
Distance to human impacts			
Distance to roads	−0.07	**0.65**	0.10
Distance to big cities (X^2)	**0.42**	**0.68**	0.03
Eigenvalues	3.31	2.02	1.66
Cumulative explained variance	0.21	0.33	0.44

Loadings larger than 0.4 in absolute value are marked in bold.

columns (environmental variables listed in Table 1), thereby creating different habitat gradients (principal components or PCs) that were taken as niche dimensions. To facilitate the interpretation of the resulting principal components, we applied a Varimax normalized rotation, an orthogonal rotation technique that minimizes the number of original variables related to each PC, ensuring that few variables have large factor loadings and many have small ones (near zero) (McGarigal *et al.*, 2000).

To create categorical habitat types along habitat gradients, the scores of the 2834 1-km^2 squares along each PC were divided into 15 classes. The first and last classes (1 and 15) were defined in terms of data distribution, being limited by the 5% and 95% percentiles. The other 13 classes resulted from equal-length divisions of the remaining 90% of the data. For each of these habitat categories, we calculated the relative occurrence of each species as the proportion of squares within a certain category in which the species had been detected, divided by the proportion of all surveyed squares in which the species occurred (Fig. 1). As a measure of species specialization, we used the standard deviation (SD) of relative species occurrences, which was calculated independently for each of the three habitat gradients (PCs). A specialized species would concentrate most of its occurrences in few habitat categories, thus having large SD values, while a generalist species would tend to occur similarly across habitat classes, thus having low SD values.

Species SD values were found to be tightly related to overall species occurrence (i.e. the total number of squares where the species had been detected; log$_{10}$-transformed) ($R^2 > 0.45$ for all

three relationships, Fig. 2). These relationships had negative slopes, implying that more common birds tended to be perceived as generalists and rare birds as specialists. Following the resource breadth hypothesis (e.g. Gregory & Gaston, 2000) it could be argued that these relationships have an ecological basis, since species with broad niches would be able to attain larger geographical distributions. To test whether the relationships between SD values and occurrence were an artefact of our approach, we repeated SD calculations 300 times using randomized matrices in which we maintained the overall frequency of occurrence of each species but randomly placed their presences among 1-km^2 squares (i.e. all species behaving as strict generalists). These analyses showed that equally generalist species were perceived as more specialized along the range of SD values when they were rarer (Fig. 2). Thus, we regressed species SD values against total species occurrences (log$_{10}$-transformed) and retained the standardized residuals as our final measures of specialization. Positive residuals would then denote higher specialization than expected from a given number of occurrences, while negative residuals would characterize generalist species. We also calculated the differences between the observed SD values and those expected for a perfect generalist occurring in the same number of squares (see Fig. 2) as another possible specialization measure. However, we discarded those measures as indices of species specialization because they were related to species occurrences. (See Appendix S1 in Supporting information for a detailed report of these results.)

We calculated species specialization indices independently for the three habitat gradients. These measures are henceforth referred to as SP1, SP2 and SP3. We used species rarity as an additional and independent measure of specialization. We calculated specific rarity indices by subtracting from 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). We finally retained SP and rarity values solely of those bird species occurring at least in 50 of the 2834 squares ($n = 103$ species).

We compiled data on the species specialization index (SSI) given in Devictor *et al.* (2008b), and calculated after Julliard *et al.* (2006), in order to compare them with our SP and rarity values. The crossing of our species list and that of Devictor *et al.* (2008b) resulted in 82 coincidences that were selected for further comparisons. We also compiled the frequency of occurrence of bird species in France from the information given in Jiguet (2001), who reported the number of sample points (EPS) in which each bird species occurred from a total 1788 EPS surveyed in spring 2001.

Indices of habitat preference

Measures of specialization do not inform us about the direction of species habitat preferences, provided that they existed. We measured the intensity of the species preferences for gradient extremes through the slope of the relationship between habitat categories (numbered following their ordinal position along gradients, 1–15) and the relative occurrence of species in each habitat category (see Fig. 1). Abrupt positive or negative slopes
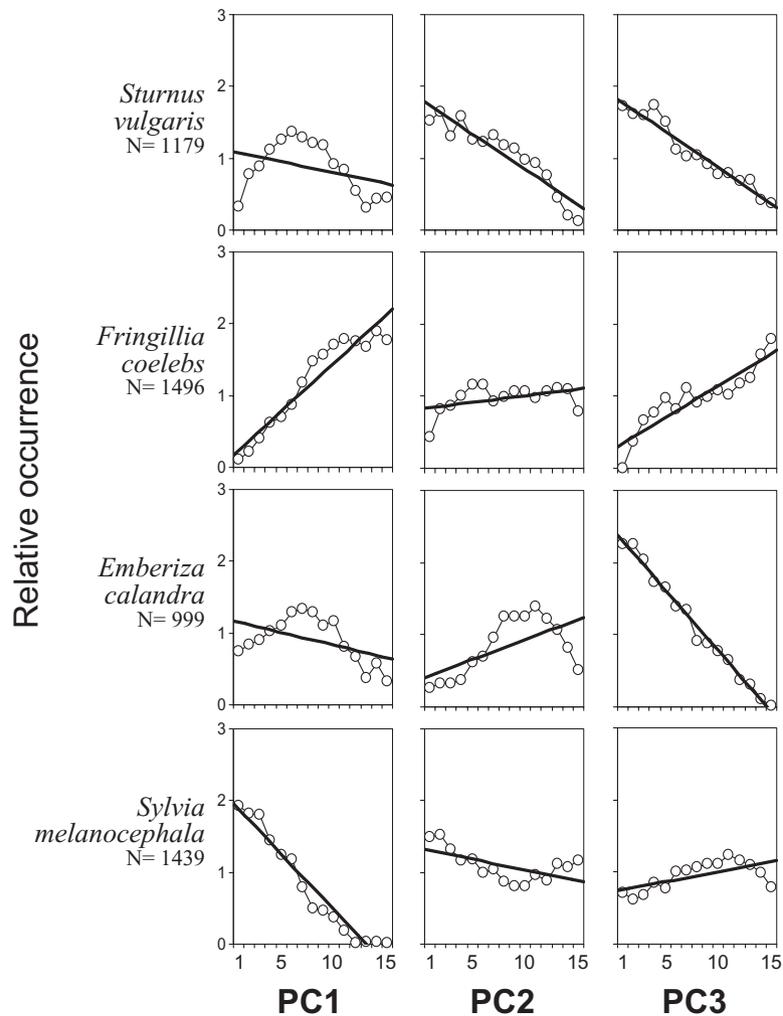
Figure 1 Four examples of the variation of relative occurrences along the three landscape gradients (PC1–3) defined by means of the principal components (PC) analysis. Each PC was divided into 15 discrete classes. Species' relative occurrence is the proportion of occurrences in each class divided by the proportion of occurrences among all surveyed squares. Specialization indices for species (SPs) were calculated from the standard deviation of relative occurrences among classes. Habitat preference measures (SLs) were calculated as the slopes of shown regression lines. Species SP and SL values were then averaged for communities to calculate CM (index of community specialization) and CMsl (mean habitat preference), respectively.

indicate preference for one of the PC extremes and are associated with specialist species, while flat slopes could be associated either with generalist species or with specialist ones showing a unimodal response along the PC. These measures can be interpreted as estimates of niche position, with the absolute values of slopes denoting the strength of preferences for landscape characteristics departing from average values (i.e. gradient extremes) (Gregory & Gaston, 2000) and their sign indicating the direction of that preference. The slopes corresponding to each species along the three PCs are henceforth referred to as SL1, SL2 and SL3.

Definition of an agricultural–forest landscape mosaic gradient

To define a habitat gradient running from agricultural to forest areas, we selected squares in which the sum of agricultural land

uses and forest cover surpassed 80% of the total square surface (Vallecillo *et al.*, 2008). The gradient was generated by subtracting the percentage cover of agricultural uses from that of forests. Thus, gradient values ranged between −100, when all land uses were agricultural, and 100, when all the square's surface was covered by forest. Squares at altitudes higher than 800 m a.s.l. were excluded from the gradient, as agricultural land uses are almost absent above that altitude. We also excluded squares in which fewer than 15 of the 103 selected bird species had been recorded (*n* = 39). The final number of squares included in the agricultural–forest gradient was 879.

In each of the squares included in the habitat gradient, we calculated indices of specialization for bird communities as the mean of SP1, SP2 and SP3 values, henceforth denoted as CM1, CM2 and CM3. Large values of these CM indices would thus denote specialist-dominated communities. Analogously, for each square we also calculated mean rarity values and average
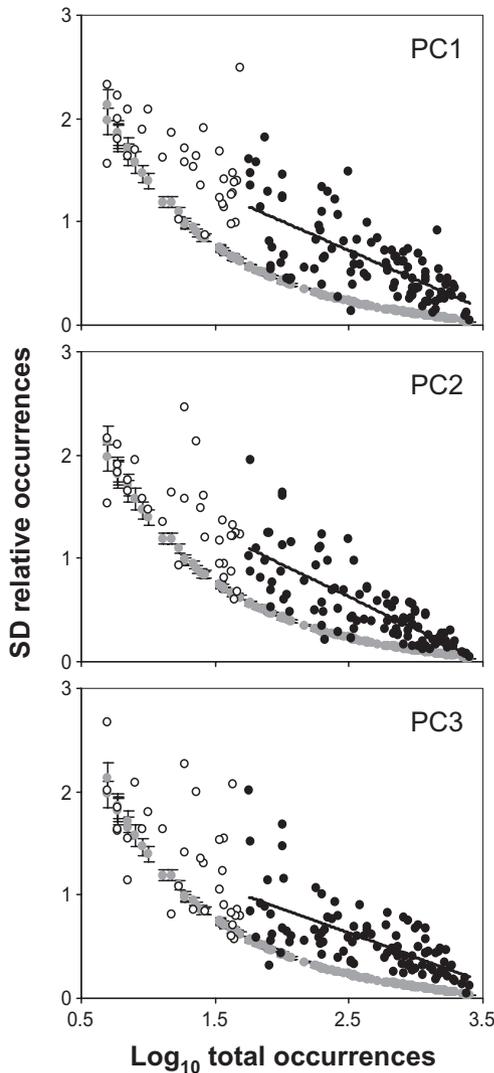
Figure 2 Relationships between the number of occurrences of bird species in Catalonia (from a total of 2834 1-km² squares) and the standard deviation (SD) in the relative occurrence of bird species along landscape gradients PC1–3 (see Fig. 1). Filled circles represent the 103 species occurring more than 50 times (regression line indicated), while empty circles correspond to less frequent species. Grey circles are the expected SD values (± 99% confidence interval) of a perfect generalist given a number of occurrences, calculated by randomly distributing bird species occurrences along landscape gradients while maintaining their frequency of occurrence. Final specialization indices for species (SPs) were calculated as the standardized residuals of shown regression lines.

SL1, SL2 and SL3 values, which were called CMsl1, CMsl2 and CMsl3. For these calculations, we considered only the 103 species with more than 50 occurrences. Changes in the indices of specialization, mean rarity and habitat preference along the habitat gradient were analysed through multiple linear regressions, using the agricultural–forest gradient and total species richness as continuous predictor variables.

In order to compare our results with the values of the community specialization index (CSI) calculated after Julliard *et al.*

(2006), we repeated CM, mean rarity and CMsl calculations considering only the 82 bird species that were found both in our list and in that of Devictor *et al.* (2008b). Again, the analyses included only squares with at least 15 bird species (from the pool of 82 species), with the resulting dataset including 864 squares. Variations of all indices (CSI, CMs, mean rarity and CMsl) along the agricultural–forest gradient were analysed through multiple regression analyses, as explained above. We analysed the relationships between CSI and the other community specialization indices (the three CMs and mean rarity) through four simple linear regression analyses and a multiple regression model using CSI as the dependent variable and all other indices as predictors.

RESULTS

Landscape gradients and indices of specialization

The first three PCs extracted from the PCA accounted for 44% of the variance of the original dataset (Table 1). PC1 defined a gradient running from drier and hotter Mediterranean climate areas to high-altitude zones with more temperate climatic conditions. PC2 had, towards its negative extreme, urban-dominated landscapes, while the characteristics of its positive extreme were less clear. PC3 constituted a gradient running from agriculture-dominated areas to forest-dominated ones.

The indices of specialization for bird species (SP values) varied between −2.47 (SP3 for the golden eagle, *Aquila chrysaetos*) and 4.28 (SP3 for the little bustard, *Tetrax tetrax*). Table 2 shows the 10 most specialist and generalist species for the different landscape gradients as well as the 10 species showing the strongest preferences for opposite gradient extremes (see Appendix S2 for the complete dataset). The three sets of SP values were positively correlated (Table 3), indicating that species tended to repeat their roles as specialists or generalists along different niche dimensions. However, these relationships, though statistically significant, were rather weak, as a given group of SP values could only explain up to 22% of the variance of any of the other two SPs. There were also some examples of a species acting as a generalist along one landscape gradient and as a specialist along another. For instance, the ortolan bunting (*Emberiza hortulana*) was one of the most generalist species along the climatic gradient defined by PC1, but one of the most specialized along the urban gradient defined by PC2 (Table 2). Interestingly, SL values along the different landscape gradients were also positively correlated (Table 3), indicating that bird species tended to show preferences either for more Mediterranean, urban and farmland areas, or for more temperate, non-urban and forest ones (see Table 2). SL and SP values along a particular niche dimension showed clear convex second-order polynomial relationships (Fig. 3). Generalist species had SL values around 0 while species showing clear preferences for gradient extremes also tended to be the most specialized.

SSI values calculated for French birds did not show significant correlations either with any of the indices of specialization in Catalonia or with the indicators of habitat preference. Only the total number of occurrences in Catalonia was positively

Table 2 Summary of the results of the indices of species specialization (SP) and habitat preference (SL).

	PC1	PC2	PC3
Specialists High SP values	Oenanthe hispanica	Turdus torquatus	Tetrax tetrax
	Emberiza citrinella	Regulus regulus	Regulus regulus
	Sylvia melanocephala	Serinus citronella	Serinus citronella
	Prunella modularis	Oenanthe hispanica	Turdus torquatus
	Galerida theklae	Prunella modularis	Parus ater
	Oenanthe oenanthe	Streptopelia decaocto	Galerida cristata
	Tetrax tetrax	Gyps fulvus	Loxia curvirostra
	Regulus regulus	Pyrrocorax pyrrocorax	Passer montanus
	Monticola solitarius	Galerida theklae	Parus cristatus
	Cisticola juncidis	Emberiza hortulana	Regulus ignicapillus
Generalists Low SP values	Circaetus gallicus	Sylvia borin	Aquila chrysaetos
	Accipiter gentilis	Falco subbuteo	Anthus campestris
	Falco peregrinus	Accipiter gentilis	Oenanthe oenanthe
	Milvus migrans	Accipiter nisus	Falco subbuteo
	Emberiza hortulana	Jynx torquilla	Accipiter nisus
	Jynx torquilla	Muscicapa striata	Accipiter gentilis
	Falco subbuteo	Corvus monedula	Sylvia communis
	Accipiter nisus	Milvus migrans	Muscicapa striata
	Anthus campestris	Motacilla cinerea	Motacilla cinerea
	Sylvia hortensis	Lanius meridionalis	Jynx torquilla
Preference for negative extreme Low SL values	Mediterranean species	Urban species	Farmland species
	Oenanthe hispanica	Streptopelia decaocto	Tetrax tetrax
	Clamator glandarius	Cisticola juncidis	Corvus monedula
	Galerida theklae	Columba livia	Coturnix coturnix
	Sylvia melanochepala	Passer montanus	Galerida cristata
	Monticola solitarius	Cettia cetti	Emberiza calandra
	Galerida cristata	Sturnus vulgaris	Milvus migrans
	Columba oenas	Pica pica	Clamator glandarius
	Merops apiaster	Motacilla alba	Passer montanus
	Cisticola juncidis	Hippolais polyglotta	Sturnus unicolor
	Sturnus unicolor	Delichon urbicum	Galerida theklae
Preference for positive extreme High SL values	Temperate species	Urban avoider species	Forest species
	Turdus torquatus	Turdus torquatus	Turdus torquatus
	Serinus citronella	Pyrrocorax pyrrocorax	Loxia curvirostra
	Prunella modularis	Oenanthe oenanthe	Dryocopus martius
	Regulus regulus	Aquila chrysaetos	Regulus regulus
	Dryocopus martius	Gyps fulvus	Serinus citronella
	Anthus trivialis	Serinus citronella	Prunella modularis
	Oenanthe oenanthe	Dryocopus martius	Parus ater
	Lanius collurio	Oenanthe hispanica	Pyrrhula pyrrhula
	Emberiza citrinella	Anthus trivialis	Regulus ignicapillus
	Pyrrhula pyrrhula	Prunella modularis	Parus cristatus

The table shows the 10 most specialist and the 10 most generalist species for the three selected landscape gradients, as well the 10 species with stronger preferences for any of the gradients' extremes.

correlated with SSI (Table 3). In fact, the number of positive EPS records in France explained up to 45% of the variance of SSI, denoting that rarer species tended to be identified as more specialized by the SSI. The significant relationship between SSI and frequency of occurrence in Catalonia would thus be a result of the positive correlation of the number of occurrences in France and Catalonia (Pearson's $r = 0.53$; $n = 82$; $P < 0.001$).

Specialist versus generalist communities along an agricultural–forest habitat gradient

There were a variety of responses to the agricultural–forest habitat gradient among the different indices of specialization for bird communities (Table 4; Fig. 4). Farmland habitats tended to have more specialist bird communities in relation to climatic

Table 3 Pearson's correlation coefficients among the different indices of specialization (SPs and rarity) and among indices of habitat preferences (SLs) for the 103 bird species occurring at least 50 times among the 2834 surveyed 1-km^2 squares.

		SP1	SP2	SP3	No. occ.		SL1	SL2	SL3
$n = 103$	SP1	–	0.47***	0.42***	–	SL1	–	0.38***	0.73***
	SP2	–	–	0.41***	–	SL2	–	–	0.27**
$n = 82$	SSI	−0.10	0.07	−0.02	0.43***		< 0.01	0.14	−0.11

The bottom row shows the correlation between all previous variables, plus the number of occurrences (No. occ.) in 1-km^2 squares in Catalonia (number of occurrences $\log_{10}$-transformed), and the species specialization index (SSI; from Devictor *et al.*, 2008b). These latter analyses were conducted for the 82 species that were both in our list of 103 species and in that of Devictor *et al.* (2008b). Significance levels are: ***$P < 0.001$; **$P < 0.01$.

conditions and had more Mediterranean-preferring species than communities in forest areas. CM2 also decreased along the agricultural–forest gradient, but this pattern was not associated with any clear change in the average habitat preference in relation to urbanization (the multiple regression model explained only 1% of the variation of CMsl2) (Table 4). Contrasting patterns were detected in relation to CM3 and CMsl3 variation (Fig. 4) as there was no linear relationship between the degree of specialization of bird communities and the agricultural–forest gradient, although the gradient was associated with a clear shift from farmland-dominated to forest-dominated bird communities. All three indices of community specialization decreased with increasing species richness, denoting that communities with lower α-diversity values were on average more specialized. Mean community rarity was lower towards the forest end of the agricultural–forest habitat gradient, and increased with higher species richness (Table 4).

The CSI calculated after Julliard *et al.* (2006) and Devictor *et al.* (2008b) showed a clear decrease along the agricultural–forest gradient, thus indicating an increase in the level of generalism of bird communities towards the forest extreme (Table 4). When we recalculated them using the occurrences of the 82 species coinciding in our list and that of Devictor *et al.* (2008b), both CM2 and mean rarity clearly decreased along the agricultural–forest habitat gradient, while a similar, though weaker, pattern was also observed in relation to CM3.

CSI values were strongly and positively related to those of CM2 and mean rarity (Fig. 5). This suggests that the CSI decrease towards the forest end of the gradient could be a result of a shift towards the dominance of urban generalist and common bird species within communities. There was also a positive, though weaker, relationship between CSI and CM3, while no relationship existed between CSI and CM1. The multiple regression model ($F_{4, 859} = 416.5$; $P < 0.001$; $R^2 = 0.66$) confirmed the independent relationships of CSI with CM2 ($\beta = 0.49$; $P < 0.001$), mean rarity ($\beta = 0.35$; $P < 0.001$) and CM3 ($\beta = 0.18$; $P < 0.001$), as well as the lack of relationship between CSI and CM1 ($\beta = 0.03$; $P = 0.13$).

DISCUSSION

Species specialization indices

The degree of specialization of organisms and their preferences for certain habitats have often been defined categorically (e.g.

generalists versus specialists; forest species versus farmland species) (e.g. Kitahara & Fujii, 2005). However, the description of specialization (or its opposite, niche breadth) and habitat associations through continuous variables would better fit the traditional niche dimension concept.

There have been two main approaches to describe niche properties as continuous variables. One is the use of multivariate analyses applied to community composition, often incorporating information on habitat variables (indirect and direct gradient analyses, respectively). The main multivariate techniques used toward this aim are the correspondence and the canonical correspondence analyses (CA and CCA), although improved methodologies were developed by Dolédec *et al.* (2000). The outputs of these analyses are the position of each species along axes of community composition (interpretable as habitat preference or niche position) and a measure of the dispersion of each species occurrence (interpretable as niche width), with generalist species having larger dispersions. This approach takes into account the gradual changes of resources along gradients (e.g. landscape gradients) instead of making artificial partitions of resources into closed categories and allows the interpretation of different niche dimensions (e.g. canonical axes). However, these estimators of each species' niche breadth are dependent on the occurrences of all other species, since ordinations are based in the specific composition of communities. Therefore, their use for subsequent analyses on generalism–specialization or functional homogenization patterns among communities could be inappropriate, due to circular reasoning and lack of independence of data. This problem is also present in a recent proposal to calculate niche width based on species co-existences (Fridley *et al.*, 2007).

A second approach, developed by Julliard *et al.* (2006), uses dispersion measures (coefficient of variation) of abundances across habitat categories, with higher dispersion being associated with more specialized species. In this case, specialization measures are created independently for each species and thus resulting values of the species specialization index (SSI) do not present dependency problems when used to calculate indicators of the degree of community specialization or functional homogenization (e.g. Julliard *et al.*, 2006; Devictor *et al.*, 2008a). Still, the process for obtaining SSI values does not consider the continuous nature of landscape gradients, using a hierarchical categorical habitat division. Therefore, indicators of habitat preferences cannot be associated with any particular SSI values, making it difficult to interpret the changes observed in the degree of
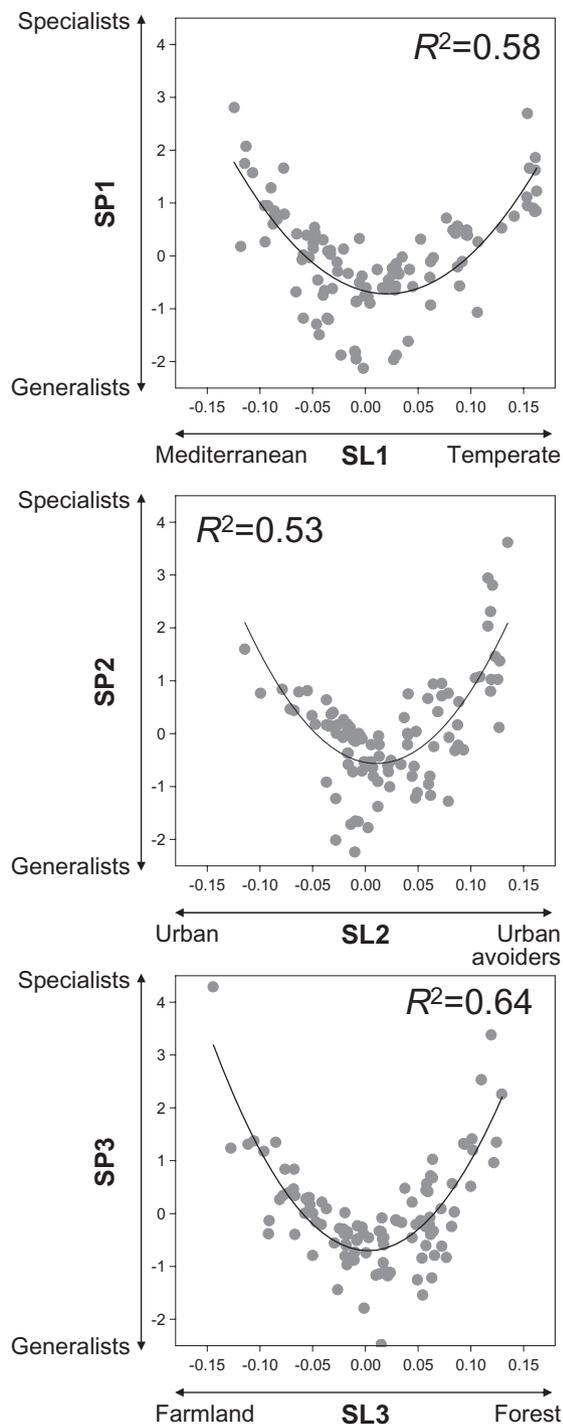
Figure 3 Relationships between habitat preference indices (SLs) and indices of specialization (SPs) for the 103 most frequent bird species in Catalonia. Lines and R^2 values correspond to second order polynomials.

specialization at the community level. For instance, Devictor *et al.* (2008a) reported almost coincident SSI values for species with contrasting habitat preferences such as the house sparrow (*Passer domesticus*) and the black woodpecker (*Dryocopus martius*), although these differences could not be numerically assessed. In the present work we adapted the methodology pro-

posed by Julliard *et al.* (2006), incorporating multivariate analyses to capture the variation in landscape characteristics and thus define orthogonal landscape gradients (i.e. niche dimensions), and creating habitat categories as portions of these gradients.

The most specialized bird species were those showing preferences for extreme habitats along any of the three landscape gradients considered here (Fig. 3). Although our approach was not incompatible with a hypothetical highly specialized species occupying intermediate portions of the landscape gradients (i.e. a strict unimodal pattern of occurrence, see Fig. 1), the general pattern was that this 'role' was rare or non-existent, and that species using the landscape's average conditions tended to be generalists. Similar results have been reported for *Protea* plants in the Cape floristic region (Thuiller *et al.*, 2004) and for spiders from central Europe (Entling *et al.*, 2007), with specialists either being relegated to extreme habitat portions through competition or occupying these extremes as true stress-tolerant species.

Functional homogenization patterns along environmental gradients

Ecological theory states that specialization should be favoured in stable systems, and that ecological perturbations would have especially strong impacts on specialist species (Futuyma & Moreno, 1988). There is an important body of evidence relating human-driven habitat alteration and destruction to the widespread decline of specialist organisms (e.g. Foufopoulos & Ives, 1999; Owens & Bennet, 2000; Julliard *et al.*, 2004). Not all species are expected to respond negatively to human perturbations, most of which benefit at least some species from the regional pool, often invasive ones and/or those with generalist habits (e.g. Futuyma & Moreno, 1988; Sol *et al.*, 2002). These generalist species that are favoured by human impacts were included by McKinney & Lockwood (1999) among the 'winners' of the present mass extinction process, while specialist species were perceived as 'losers'. The non-random pattern of species turnover due to human activities, with loser species being replaced by winner species, has been proposed as the main mechanism promoting the functional homogenization of communities (Olden & Rooney, 2006; Devictor *et al.*, 2008a). However, there are still few available quantitative analyses of functional homogenization patterns (e.g. Smart *et al.*, 2006) and their relationship with human disturbance gradients (but see Devictor *et al.*, 2007, 2008a).

Previous works have shown that habitat disturbance and fragmentation (Devictor *et al.*, 2008a) and urbanization (Devictor *et al.*, 2007) promote functional homogenization of bird communities. A general pattern extracted from these works is that perturbed or humanized areas tend to be occupied by generalist-dominated bird communities. As stated above, these patterns were interpretable as the community-level results of the higher sensitivity of specialist species to human impacts on landscapes, but our results show that contrary patterns are also possible. Along the environmental gradient we analysed, the agricultural extreme should be considered the 'humanized' or 'perturbed' one while the forest extreme would correspond to more 'natural'

Table 4 Results of the multiple linear regressions analysing the effects of the agricultural–forest gradient and community species richness on indices of community specialization (CM1–3 and CSI), mean rarity, and mean habitat preferences (CMsl1–3).

Dependent variable	Predictor variables	Whole dataset $n = 879$ 1-km^2 squares			Reduced dataset $n = 864$ 1-km^2 squares		
		β	P	Adj. R^2	β	P	Adj. R^2
CM1	Agricultural–forest	−0.42	***	0.24	0.09	*	0.01
	Species richness	−0.23	***		−0.06	0.07	
CM2	Agricultural–forest	−0.48	***	0.26	−0.68	***	0.46
	Species richness	−0.15	***		0.04	0.14	
CM3	Agricultural–forest	−0.005	0.88	0.10	−0.23	***	0.08
	Species richness	−0.31	***		−0.18	***	
Mean rarity	Agricultural–forest	−0.46	***	0.27	−0.44	***	0.31
	Species richness	0.25	***		0.36	***	
CSI	Agricultural–forest	No data			−0.64	***	0.41
	Species richness				0.03	0.25	
CMsl1	Agricultural–forest	0.78	***	0.63	0.72	***	0.53
	Species richness	0.14	***		0.11	***	
CMsl2	Agricultural–forest	−0.11	**	0.01	0.03	0.38	0.001
	Species richness	−0.06	0.075		−0.01	0.66	
CMsl3	Agricultural–forest	0.85	***	0.73	0.84	***	0.72
	Species richness	0.09	***		0.06	**	

Regressions were performed using two datasets. Community values from the whole dataset were obtained by averaging the values of the 103 most frequent bird species in Catalonia (see Appendix S1). The reduced dataset used only data for the 82 bird species that coincided in our list and in that of Devictor *et al.* (2008b) (see Table 3). In both cases, all 1-km^2 squares included in the analyses had at least 15 species. Significance levels of standardized regression coefficients (β) are: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.

areas. However, whenever we detected any clear relationship between the average degree of specialization of bird communities and the agricultural–forest gradient, forest communities were found to be more generalist (see Fig. 4).

Although our results were consistent and repeated for different indices of specialization, it would be interesting to compare these patterns with those emerging when using abundance data (see Kerbiriou *et al.*, 2009). La Sorte & McKinney (2007) showed that temporal patterns of taxonomic homogenization of North American avifauna were stronger when using abundance data than when considering only occurrences, since abundance data highlight the role of few generalist bird species that have been able to attain high densities by benefiting from anthropogenic activities. Both abundance (e.g. Devictor *et al.*, 2008a) and presence/absence (Kerbiriou *et al.*, 2009) data have been used to analyse functional homogenization of communities, but the possible influence of the use of these different data sources in the detected patterns remains to be quantified.

We found that species-rich bird communities are on average more generalist than poorer ones. As shown in Fig. 3, species with preference for extreme portions of environmental gradients have the narrowest niches, while species richness also tends to be smaller on such gradient extremes. Regarding the agricultural–forest gradient under analysis, and using the gradient categorization shown in Fig. 4, species richness was clearly lower both at the farmland and the forest end than in any of the intermediate gradient portions [one-way ANOVA, Tukey honestly significant difference (HSD) for unequal sample size; $P < 0.001$ in all cases], while there was no difference in richness between gradient extremes (Tukey HSD; $P = 0.98$). Thus, the negative relationship between richness and specialization could be related to the effects of environmental constraints simultaneously limiting the richness of communities and the niche breadths of species composing them. A similarly negative relationship, though temporal instead of spatial, was found by Kerbiriou *et al.* (2009) when analysing the evolution of the bird fauna in Ouessant Island (France), where a clear increase in species richness was coupled with a decrease in average community specialization.

These negative relationships between species richness and community specialization are apparently contrary to previously published results. Smart *et al.* (2006) showed that reductions in plant species richness, whether recorded in time (in a 20-year period) or in space, were associated with a reduction in trait diversity, which could be interpreted as an increase in the functional similarity of communities. More strikingly, in the same study area as ours, Carnicer *et al.* (2008) showed that specialized bird species tended to be present in species-rich communities, while poorer communities were mainly composed of generalist species. The apparent contradiction between these latter results and ours could be related to the methodological differences in both works. Carnicer *et al.* (2008) restricted their analyses to forest bird communities and included a large altitudinal gradient (up to 3000 m a.s.l.; see also Carnicer *et al.*, 2007), while we used only areas under 800 m a.s.l. Bird communities in Catalonia tend to be more forest-dwelling with increasing altitude (linear regression between altitude, 20–2000 m, and CMsl3; $R^2 = 0.44$; $n = 2834$; $P < 0.001$), and thus differences in the
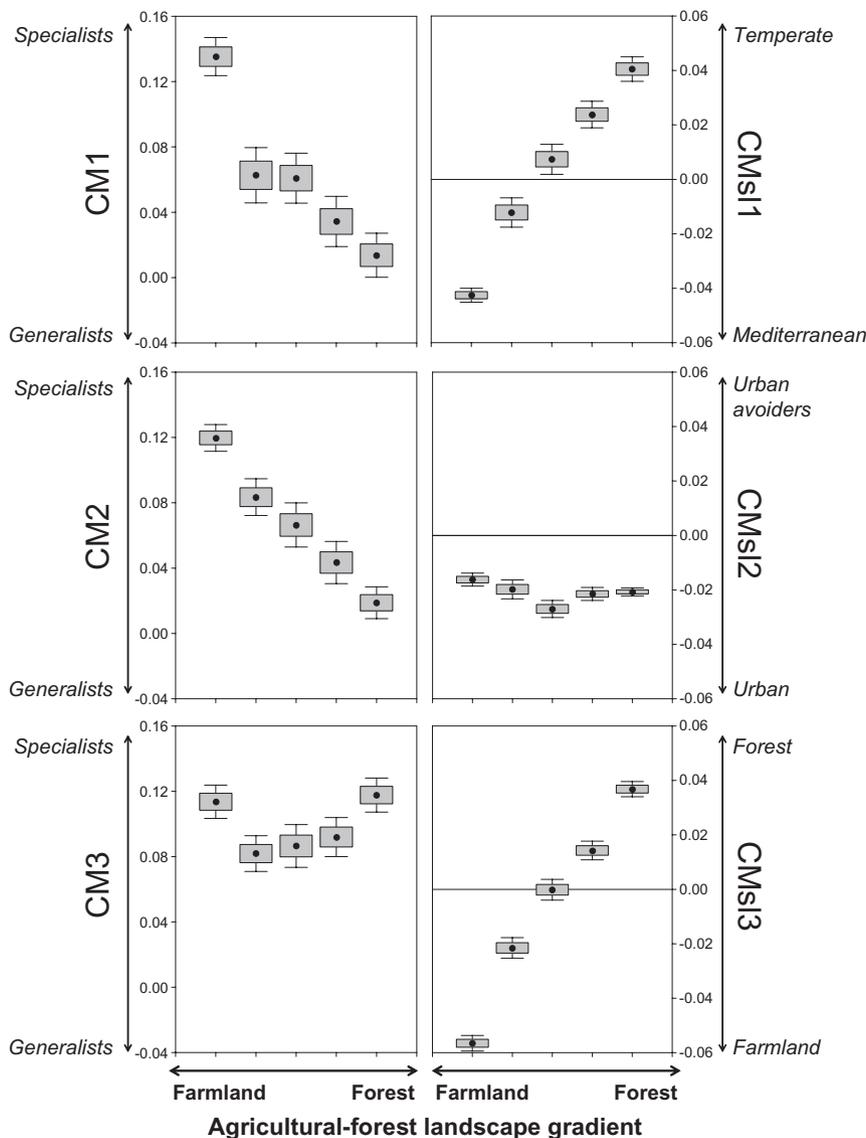
Figure 4 Variation of bird community indices of specialization (CMs) and mean habitat preference (CMsl) for the different niche dimensions along the agricultural–forest gradient. The gradient was generated by subtracting the percentage cover of agricultural uses to that of forests in 879 1-km² squares. Gradient classes are (−100, −75), (−75, −25), (−25, 25), (25, 75) and (75, 100). Middle points are mean values, boxes indicate standard errors (SE) and whiskers indicate 95% confidence intervals (i.e. 1.96 × SE).

communities and altitudinal bands under analysis could explain the contrasting results. Furthermore, Carnicer *et al.* (2008) used a single estimate of niche breadth that, as with SSI in Julliard *et al.* (2006), was probably related to each species' frequency of occurrence. If that was the case, results presented by Carnicer *et al.* (2008) would be in line with our finding that average rarity tends to increase with increasing species richness.

The Mediterranean basin has experienced thousands of years of human landscape modification for livestock and agricultural purposes, with the creation of widespread open areas in previously forest-dominated lands (Blondel & Aronson, 1999). Contrary to general assumptions on the relationships between biodiversity and habitat degradation, maximum diversity of Mediterranean bird communities did not occur in primeval forests but in human-generated agro-sylvo-pastoral landscape mosaics, which are often occupied by open habitat bird specialists (Farina, 1997; Blondel & Aronson, 1999). On the other hand, there is an almost complete lack of birds of Mediterranean origin in Mediterranean forests, which include, especially in

their western extreme, an impoverished subset of the forest bird species from western Eurasia, many of them being habitat generalists able to occupy a wide variety of forest environments (Covas & Blondel, 1998). Moreover, migrant bird species breeding in Europe have been shown to favour open habitats, a pattern that is interpreted as an evolutionary conservation of niche properties of long-migrant species that originated in tropical Africa (Böhning-Gaese & Oberrath, 2003). All these arguments are in line with our results, which show that farmland areas bear more specialized bird communities than forest habitats.

Rural depopulation and land abandonment have favoured the rapid expansion of forest in Mediterranean areas in the last century (Debussche *et al.*, 1999; Suárez-Seoane *et al.*, 2002). This pattern is also clear in Catalonia, where forest cover has continuously increased in the last decades, even though large forest extensions have been burned by wildfires (Brotons *et al.*, 2004; Vallecillo *et al.*, 2008). As a result of this situation, open habitat specialist bird species are suffering generalized declines
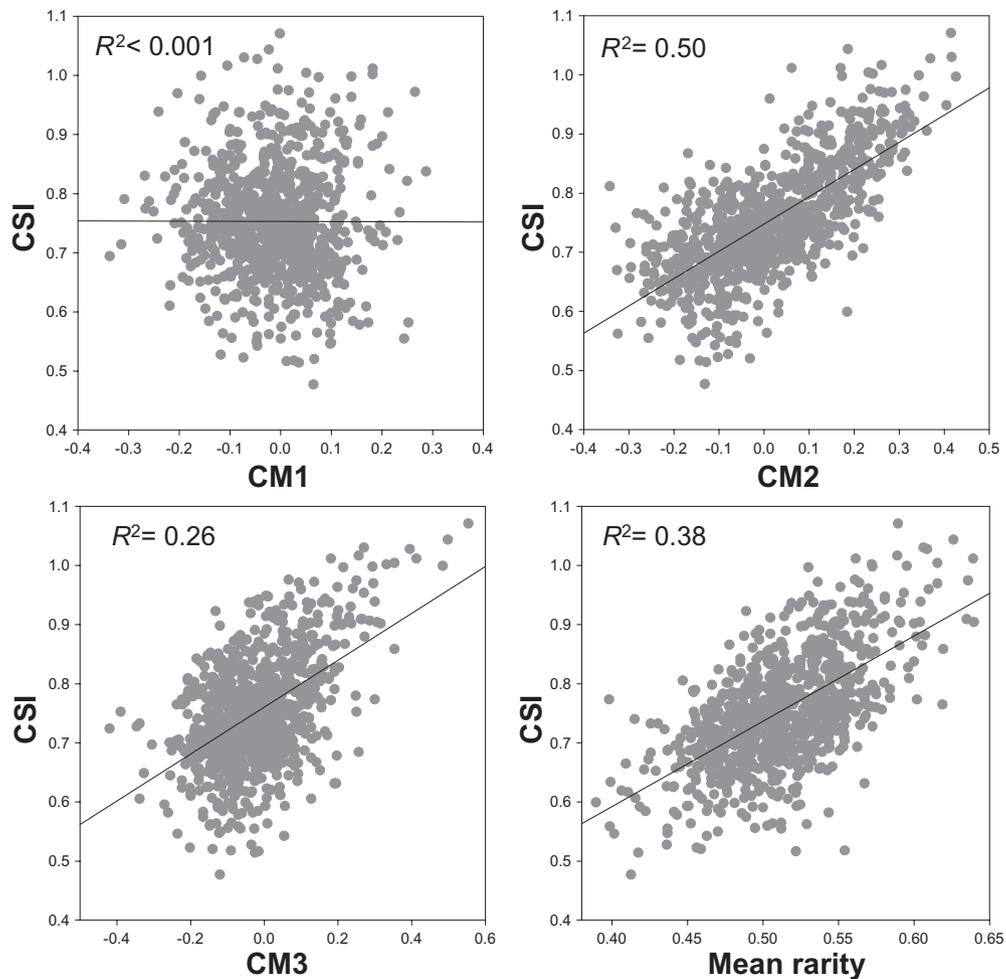
Figure 5 Linear relationships between community indices of specialization (CMs) and mean rarity and the community specialization index (CSI) calculated after Julliard *et al.* (2006) and Devictor *et al.* (2008b).

in Mediterranean areas (De Juana, 2004) but also across Europe (Gregory *et al.*, 2004). Previous work had shown that bird richness in Mediterranean areas is enhanced in the heterogeneous landscapes generated by agricultural activities (e.g. Farina, 1997). As a novelty, our results also suggest that landscape homogenization produced by forest expansion in Mediterranean areas is promoting functional homogenization of bird communities, by favouring generalist-dominated forest communities.

Indicators of functional homogenization

Devictor *et al.* (2008a) proposed the use of the CSI as a biodiversity indicator to identify processes of functional homogenization related to human impacts. These authors argued that, contrary to other biodiversity indicators, the CSI is ecologically meaningful, being able to reflect the substitution of specialists by generalist species (e.g. McKinney & Lockwood, 1999), and that it can be related to different human impacts (e.g. Devictor *et al.*, 2007). Although we agree with these ideas, we believe that our approach to the description of functional homogenization could be used as a more interpretable set of indicators of community

responses to environmental change, for two main reasons. Firstly, the changes in the mean specialization in bird communities can be related to specific landscape gradients (i.e. niche dimensions). Secondly, these changes can be explained in terms of mean habitat preferences of species occurring in bird communities. Devictor *et al.* (2008a) pointed out that large CSI values (i.e. specialized communities) could occur in highly degraded environments (e.g. specialized urban bird assemblages), thus violating the basic assumption of the functional homogenization indicator that the presence of specialists would be a signature of good environmental integrity. Our multidimensional approach to the description of community specialization would be able to identify such situations, due to the specificity of each one of our community specialization estimators.

The utility of indicators of functional homogenization can be influenced by the site specificity of the specialization estimators (Entling *et al.*, 2007; Devictor *et al.*, 2008a). Bird data from Catalonia offer a good opportunity to analyse habitat specialization at the landscape scale, due to the high diversity of environmental conditions (in relation to climate, orography, vegetation cover and land uses) recorded in a relatively small territory. Nevertheless, there are certain species that may be perceived as specialist

in Catalonia just because there they are near the bounds of their distribution range. This is true for some species having their main distribution range towards the south (e.g. blue rock thrush, *Monticola solitarius*) as well as for others that are widespread in more northern areas (e.g. common goldcrest, *Regulus regulus*). Our results showed that the inclusion or exclusion of species near the limits of their core areas can have strong effects on the perception of functional homogenization along environmental gradients. For instance, the relationship between CM1 and the agricultural–forest gradient lost its significance when reducing the species list to 82 species (see Table 4) due to the deletion of a group of Mediterranean species (e.g. black-eared wheatear, *Oenanthe hispanica*, great spotted cuckoo, *Clamator glandarius*, or Thekla lark, *Galerida theklae*; see Table 2].

It would be therefore desirable to work on large-scale indicators of species habitat specialization and of functional homogenization of communities, something that would imply the sharing of datasets on bird distribution from several areas. In Europe, separate indicators would probably be necessary for the different biogeographic regions (EEA, 2002). We agree with Devictor *et al*. (2008a) in that functional homogenization indicators, which are firmly based in niche theory, would be more ecologically sound estimators of biodiversity trends under different pressures. In our study example (the agricultural–forest gradient), an indicator of functional homogenization for the Mediterranean biogeographical region would be a useful tool to determine the large-scale fate of bird biodiversity in the area under the present land abandonment and forest expansion scenario.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Comparison of regression residuals and observed–expected approaches to calculate occurrence-independent specialization measures.

Appendix S2 List of the indices of specialization (SPs) and habitat preference (SL) for 103 bird species.

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