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When species become generalists: on-going large-scale changes in bird habitat specialization

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ABSTRACT

Aim Species specialization is often considered as a stable species characteristic over the short term. However, this assumption has hardly been tested, even though it may impair our ability to track the impoverishment of biodiversity induced by the rapid replacement of specialists by generalists. We tested whether species specialization in birds varied over a short period of time, and assessed whether variations in species specialization influence community-level metrics of biotic homogenization.

Location France.

Methods We studied the variations in specialization to habitat closure of 94 bird species over the period 2002–08, accounting for species variations in mean density, habitat preference and migratory status. We then quantified the temporal changes in a community specialization index, which measures functional homogenization.

Results Specialization decreased over time for 35 species (37%), while 46 (49%) showed non-significant negative trends and 13 (14%) had null or non-significant positive trends. The more a species was specialized at the beginning of the study, the more it generalized. We additionally found that changes in the specialization level were density dependent: 34 species (36%) became more generalist in years of higher densities while only one became more specialized. At the community level, accounting for this inter-annual variability in species specialization accentuated the trend in the functional homogenization of bird communities.

Main conclusions Habitat specialization is a labile ecological trait, which may change in the short term following habitat degradation, density dependence and source–sink dynamics. Accounting for short-term temporal variations in observed habitat specialization of species can increase our understanding of the effects of global changes on species strategies and community dynamics.

Keywords

Bird communities, functional homogenization, global changes, habitat gradient, specialization, temporal variations.

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INTRODUCTION

Specialization can be quantified by measuring the narrowness of a species' use of a particular gradient of resource or habitat (Devictor *et al.*, 2010). Indeed, the ecological niche theory predicts that specialists should tolerate a narrower array of resource levels than generalists, and are thus expected to be less able to cope with environmental changes that affect the avail-

ability of the resources (Levins, 1968). In the current context of unpredictable and rapid global changes, habitat specialists should be more negatively affected than generalists (Colles *et al.*, 2009), resulting in a world-wide homogenization of communities. This has been empirically supported for a variety of taxonomic groups including insects (Brouat *et al.*, 2004), fishes (Wellenreuther *et al.*, 2007) and birds (Devictor *et al.*, 2008a,b).

Alternatively, species may also adapt to environmental modifications by changing their own level of specialization. Most of the studies addressing the issue of niche changes have investigated how shifts in one or more axes of the niche may lead to local adaptations or speciations at evolutionary time-scales (Futuyma & Moreno, 1988; Colles *et al.*, 2009). This approach reflects the effect of gradual, long-lasting changes in the resource gradients which favour differential resource exploitation among co-occurring subpopulations of the same species. Less attention has been paid to niche stability in the short term, say a few years or decades (Devictor *et al.*, 2010). Such small time periods are usually considered to be too short to allow environment-based microevolutionary selection, although some examples of rapid evolution do exist (Pulido & Berthold, 2004). Therefore, specialization has most often been deemed as a fixed attribute of species or individuals in the short term (Thompson, 1998; Bolnick *et al.*, 2003; Holt, 2009). However, whether specialization is fixed or labile over short periods of time is still unclear. It is sensible to assume that no or only very slight short-term shifts occur in the fundamental niche characteristics of species, as they should mostly be driven by natural selection. The costs linked to microevolution or plasticity should also keep the realized niche stable over the short term (Dall & Cuthill, 1997). However, changes in realized niche breadth irrespective of variations of the fundamental niche could also be influenced by factors that vary substantially over short periods of time, such as climatic conditions, competition or predation. While assessments of changes of in the fundamental habitat specialization of species are blurred by various confounding factors, changes in a species' realized specialization can easily be quantified from field surveys (Devictor *et al.*, 2010).

Regional population sizes influence local population dynamics (Gaston & Blackburn, 2000), and conversely, local population processes partly determine abundances at larger spatial scales (Freckleton *et al.*, 2005). The scaling between local and regional population sizes depends on interactions between population growth rate, intra-specific competition and density dependence (Maurer & Taper, 2002), which are in turn influenced by species-specific characteristics such as life span, migration strategy, reproductive success or specialization (Saether & Engen, 2002). For a given increase in regional population size, generalist species should consistently increase locally across their range as they are able to thrive in a broad range of habitats; similarly, density dependence and source-sink population processes should influence the carrying capacity of a population in optimal habitats, and in turn determine abundance in suboptimal habitats (Pulliam, 1988, 2000; Dunning *et al.*, 1992; Maurer & Taper, 2002). In such situations, the apparent specialization may decrease or increase without necessarily being accompanied by a change in the species' fundamental niche (Taylor, 1961). Hence, investigating temporal shifts in the realized specialization of species may provide interesting insights into the strength of density dependence and into a species' plasticity to rapid environmental changes.

Beyond the changes in specialization at the species level, changes in species niche breadth are also likely to affect inter-

specific interactions, and consequently the structure and dynamics of species assemblages (Hughes, 2000; Mouillot *et al.*, 2007; Devictor *et al.*, 2010). In this respect, community-level specialization indices can be useful: in accounting for the relative abundance of a specific trait (e.g. specialization), such functional descriptors are more meaningful than classical metrics (e.g. species richness; McGill *et al.*, 2006). Ideally, these metrics should be designed to account for both long- and short-term variations in their underlying processes. For instance, the rapid homogenization of bird communities, due to a decrease in the abundance of specialists coupled with an increase in generalists, reflects the dynamics of winners and losers in the face of global changes (Devictor *et al.*, 2008a). However, the differential population trends between generalists and specialists could be compensated for (or increased) by an overall trend of the species to become more specialist (or generalist) over time.

We explored the short-term temporal variations (2002–08) of realized habitat specialization in birds. Birds are well suited for such an analysis due to their rapid response to changes in their environment (e.g. Crick, 2004, climate; Devictor *et al.*, 2008a, landscape). As they exhibit various strategies, and because the availability of food and nesting sites varies considerably among habitats, measuring birds' habitat specialization is an effective way to summarize many dimensions of their ecological niches. As common birds are known to segregate along a gradient of vegetation structure (Berg, 1997, 2002), we chose to build our specialization index over a gradient of habitat openness ranging from open fields to closed mature forest. We addressed three questions within this framework: (1) is specialization to habitat openness a fixed trait in the short term, (2) are any existing short-term variations in specialization density dependent at a large spatial scale, and (3) do short-term variations in the degree of specialization (if any) contribute to the current biotic homogenization of bird communities? Our results suggest that the on-going biotic homogenization in bird communities, which results from more favourable population trends for generalist species, is being accentuated by a generalization of individual species themselves.

MATERIALS AND METHODS

Bird data

Data collection

We used data from the French Breeding Bird Survey (FBBS), a standardized monitoring programme in which volunteers count breeding birds at fixed sites, year after year (Julliard & Jiguet, 2002). We restricted our study to the period 2002–08 for which the sampling effort was substantial and widely distributed at the national level (Fig. 1; for the number of points per year see Table 1 in Appendix S1 in Supporting Information). Most of the points had a relatively short lifetime (mean \pm SD = 3.55 \pm 1.99 years).

In this survey, a 2 \times 2 km plot was randomly selected within a radius of 10 km from a locality provided by each observer. In

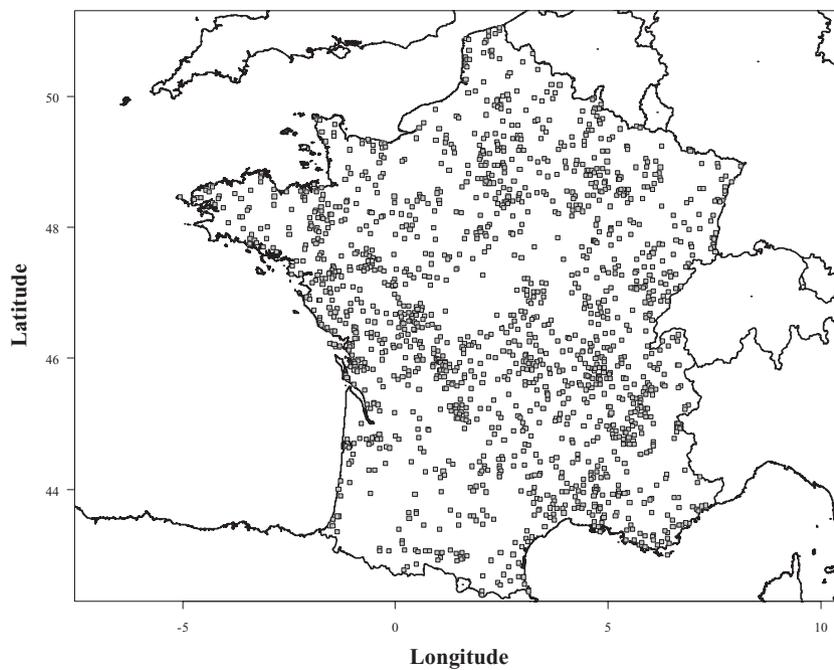


Figure 1 Map of the 2 × 2 km French Breeding Bird Survey plots surveyed at least once during the period 2002–08 and which provided data for at least 1 of the 94 species considered in our study. Each plot contains 10 point counts distributed homogeneously across available habitats.

Table 1 Model selection results (models including either year, *Y_n*, or density, *D_n*). All tested models are presented; the Δ AIC is calculated with respect to the best model, indicated in bold characters. *K* is the number of estimated parameters in each model. All models also include nested taxonomic random effects (genus/family/order).

Model	Expression	<i>K</i>	AIC	Δ AIC
S	sp	94	588.6	196.7
Y1	yr	2	1128.8	736.8
Y2	sp+yr	95	450.8	58.8
Y3	sp+yr+(sp:yr)	188	455.4	63.4
Y4	sp+yr+(yr:SSI02)	96	413.8	21.8
Y5	sp+yr+(yr:SSI02)+(yr:hab)	97	398.0	6.1
Y6	sp+yr+(yr:SSI02)+(yr:hab)+(yr:mig)	98	392.0	0.0
Y7	sp+yr+(yr:SSI02)+(yr:hab)+(yr:hab:SSI02)+(yr:mig)	99	392.2	0.2
D1	log(de)	2	620.0	238.6
D2	sp+log(de)	95	390.1	8.7
D3	sp+log(de)+(sp:log(de))	188	406.5	25.1
D4	sp+log(de)+(log(de):SSI02)	96	384.6	3.2
D5	sp+log(de)+(log(de):SSI02)+(log(de):hab)	97	381.4	0.0
D6	sp+log(de)+(log(de):SSI02)+(log(de):hab)+(log(de):mig)	98	383.4	2.0
D7	sp+log(de)+(log(de):SSI02)+(log(de):hab)+(log(de):hab:SSI02)+(log(de):mig)	99	385.3	3.9

AIC, Akaike Information Criterion; sp., species (factor); yr, years (continuous); SSI, Species Specialization Index; SSI02, SSI of year 2002 (continuous); hab, habitat (factor, either ‘closed’ or ‘open’); mig, migratory status (factor, either ‘short distance’ or ‘long distance’); de, density (continuous).

each plot, the observer distributed 10 count points in order to best represent the diversity of occurring habitats. Counts were performed twice a year at an interval of 4 to 6 weeks, before and after 8 May, allowing sampling of early singing species as well as late migrants, and to cover a wide variety of habitats. Each visit consisted of a 5-min point count, carried out between 1 and 4 h after sunrise, in which all birds detected (either seen or heard, excluding those flying over) within a 100-m radius of the observer were recorded. We excluded raptors and most wetland birds for which our habitat gradient was not relevant, and

because they are not well sampled by this survey design. Plots from alpine areas were excluded as their number was limited in all years, leading to temporal heterogeneity in their distribution. The influence of altitude on habitat openness may also result in confusing habitat specialization and the dependence of species on mountain climatic conditions.

For each species recorded, in each of the 7 years (*n* = 94 species; Appendix S2), we retained the mean density of individuals over the two annual visits at each point. Using the mean rather than the maximum density limits the effect of transient

birds that sing temporarily but do not breed. As the sedentary species considered are most likely to still be singing at the time of the second visit this calculation should not underestimate their occurrence.

Habitat gradient

Observers provided a classification of the habitat within 100 m around each point, according to a hierarchical description adapted from Crick (1992). The first level corresponds to a division into four categories (farmland, natural, urban and other types of habitats) completed by a simple characterization of the main vegetation structure and composition. We excluded points in wetlands and bare rock areas, which do not correspond to the explored gradient, but kept points in urban forests. We focused on a gradient between closed (dense mature forest) and open habitats (open agricultural lands) derived from this classification (see Appendix S3 for the detailed habitat classification). Classes 1 to 4 referred to mainly forested areas ordered by structure, from mature stands (class 1) to young forest stands of less than 3 m in height (class 4). Classes 5 to 8 corresponded to open areas, from agricultural landscapes with tree-planted edges (class 5) to open fields (class 8).

Volunteers were asked to describe their points each year; however, habitat description was missing in some years for 30% of the surveys. We thus controlled for potential bias linked to unreported or undetected habitat changes (see Appendix S1 for details and discussion on this issue).

Specialization indices

Species specialization index

We used the Species Specialization Index (SSI), which has been proposed as a robust specialization metric for birds (Devictor *et al.*, 2008b) and valuably used with the FBBS dataset (Julliard *et al.*, 2004, 2006; Devictor *et al.*, 2007, 2008b). This index assumes that the more abundant a species is in certain habitat classes with respect to the other classes, the more specialized it is. Thus, the SSI of a given species i at year j is the coefficient of variation of its densities across the k habitats considered ($k = 8$ in our case), following the approach of Julliard *et al.* (2006):

$$SSI_{i,j} = \frac{SD(d_{i,j,k})}{d_{i,j,k}}, \text{ where SD refers to standard deviation.}$$

As our aim was to explore the temporal variations of the SSI at a large spatial scale, we based each species' annual SSI on the mean density $d_{i,j,k}$ in each of the eight habitat classes k (Appendix S3b):

$$d_{i,j,k} = \frac{\sum_{p=1}^{n_k} d_{i,j,k,p}}{n_k}$$

where $d_{i,j,k,p}$ is the density of species i , at year j , on point p which belongs to habitat class k ; and n_k is the number of points in class

k . Thus, potential variations in the number of points per class were accounted for in the calculation of the species-level indices; we also controlled for a potential bias on the SSI arising from small sample sizes (see Appendix S1d). The SSI values averaged by species over the 7 years ranged from 0.22 (blackbird) to 2.64 (great reed warbler) (mean = 1.27 ± 0.60 , $n = 94$ species).

Community specialization index

To assess the influence of temporal change in SSI when quantifying the homogenization of bird communities towards more generalist species, we calculated the Community Specialization Index (CSI; Julliard *et al.*, 2006) as the average SSI of all individual species occurring at a count point, weighted by the density of the species at that point:

$$CSI_{j,p} = \frac{\sum_{i=1}^{s_{j,p}} (d_{i,j,p} \times SSI_{i,j})}{\sum_{i=1}^{s_{j,p}} d_{i,j,p}}$$

where $SSI_{i,j}$ is the SSI of species i at year j , $d_{i,j,p}$ is the density of species i in year j at point p and $s_{j,p}$ is the number of species at point p in year j . We calculated the CSI for each point count and year, considering the SSI as either a fixed (using the SSI of the year 2002) or a time-varying attribute (using each yearly SSI).

Data analysis

Temporal trends in the SSI

As a first step, we calculated the trends in the SSI for each species over 7 years, using simple linear regressions with the annual SSI as a response and year or log(density) as explanatory variables. This allowed us to explore trends in each species' specialization separately.

The second step was to build a multi-species model structure, with the SSI of species i in year j as a response variable. Because we needed to quantify the inter-specific variations of the specialization, we included species_{*i*} as a fixed effect in each model. Species closely related in phylogeny could vary similarly in their specialization, violating the independence assumption. Hence, we accounted for the possible clustering of specialization across species by adding order, family and genus as nested random effects on the intercept to all the models, following the taxonomic order proposed by Gill & Donsker (2010). A finer correction for phylogeny would have necessitated a completely resolved phylogenetic tree for all the species considered, which is not yet available.

The aim of this multi-species model was to describe: (1) the temporal variations of the SSI, and (2) to relate the SSI to species annual density. As there is only one measure of mean density per year and per species, adding both terms in a single model would not be relevant. Hence, we chose to build a model with a year effect (M_{Year}) and another with a density effect (M_{Density}). In the

density model, we used the species mean annual densities (log transformed), all habitats combined, to describe potential density dependence on temporal variations of specialization.

Additional terms in our two multi-species models were fixed linear terms at the species scale, and relevant interactions between them. Because we wanted to test whether the temporal changes in SSI were linked to an initial level of specialization of the species, we entered the SSI of the year 2002 (SSI_{02i}) as the ‘baseline SSI level’. We also included in both models the species’ migratory strategy (‘mig_i’) with two levels according to the EBCC’s classification (<http://www.ebcc.info/index.php?ID=125>, Gregory *et al.*, 2005), ‘short-distance migrant’ and ‘long-distance migrant’. Indeed, as the climatic conditions adversely affecting short-distance and long-distance migrants differ (Forchhammer *et al.*, 2002), temporal trends in breeding densities may differ according to migration strategy, affecting in turn temporal changes in the SSI. We defined each species’ habitat preference (‘habitat_{ij}’) according to the barycentre of densities across the eight habitat classes. The barycentre of species *i* at year *j*, $G_{i,j}$, was taken as its mean habitat, weighted by its densities in year *j* in each habitat of the gradient:

$$G_{i,j} = \frac{\sum_{k=1}^K (\text{hab}_k \times \overline{d_{i,j,k}})}{\sum_{k=1}^K \overline{d_{i,j,k}}}$$

where hab_k is the *k*th class of habitat (from 1 to 8), and $d_{i,j,k}$ is the mean density of species *i* during year *j* in habitat class *k*. We classified species with a habitat barycentre under 5 (i.e. from mature forest to young stand) as ‘closed habitat species’ and others as ‘open habitat species’. Habitat 5 was included in ‘closed habitat’ as it consists of young forest stands with few open spaces, and located in a forested matrix. To complete the two main models, we introduced interactions between $X_{i,j}$ (being either the year or density effect) and habitat, $X_{i,j}$ and migratory status (mig_i), $X_{i,j}$ and SSI_{02i} , and, $X_{i,j}$, SSI_{02i} and habitat. The maximum model structure was thus:

$$SSI_{i,j} = \text{species}_i + X_{i,j} + (\text{habitat}_{i,j} : X_{i,j}) + (SSI_{02i} : X_{i,j}) + (\text{mig}_i : X_{i,j}) + (X_{i,j} : \text{habitat}_{i,j} : SSI_{02i}).$$

We constructed all the relevant submodels nested in the M_{Year} and M_{Density} model structures (listed in Table 1). We fitted the models using the maximum likelihood estimator rather than restricted likelihood because fixed effect structures varied between candidate models (Wood, 2006).

The relevance of R^2 for mixed models is still being debated (Orelien & Edwards, 2008), hence we used an information criterion approach to compare candidate models. We selected the model with the lowest Akaike Information Criterion (AIC) among each set, a selection method which penalizes the likelihood of models with large numbers of parameters (Burnham & Anderson, 2002). Finally, we tested for the dependency of our final model on the SSI of year 2002. Indeed, stochastic fluctuations of densities across habitat could make species appear more

specialized than they are by chance only, leading to a spurious negative trend in specialization over the period. Details of the methods and results regarding this bias are provided in Appendix S4.

Temporal trends in densities

We tested whether a temporal trend in density existed among our sample of 94 species, and whether the level of specialization depended on this trend, by building one additional model (‘trend model’), with log(density) as the response variable, and year, SSI_{02i} , and year $\times SSI_{02i}$ as explanatory variables, and species as a random effect.

Temporal trends in the CSI

We looked at the temporal variability of the CSI through a generalized linear mixed model with CSI (calculated at each count point) as the response variable, year as a fixed factor, and 2×2 km plot (see Data Collection in the Bird Data section) as a random effect on the intercept of the model to account for the non-independence of points.

To assess whether and how the observed temporal variation in the CSI was linked to the dynamics of specialists and generalists (Devictor *et al.*, 2008b), and/or to the variation of the individual species’ specialization, we conducted a two-step analysis:

1. We calculated the trend in CSI based on the SSI of 2002 (CSI_{02}).
2. We then calculated the trend in CSI based on yearly SSI values (seven values of SSI for each species, CSI_y).

The CSI_{02} assumes a temporally fixed specialization level for each of the 94 species. Hence, it only accounts for temporal changes in species composition at the point level, which corresponds to an assessment of the winners–losers dynamics proposed as a major consequence of biotic homogenization. On the other side, CSI_y also considers within-species variations of specialization: it does not only reflect differential dynamics between species with different specialization levels but also the influence of the yearly changes in each species’ specialization. If community specialization varied only with respect to changes in community composition, temporal trends in CSI_y and CSI_{02} should be similar (i.e. no effect of variations in species specialization). Conversely, differential trends between both indices would mean that community specialization is not driven only by species dynamics, but also by changes in species specialization.

Finally, as the study plots are clustered to some extent (Fig. 1), one could also expect a spatial dependency between trends in the specialization of communities at neighbouring points, which may affect the overall trend over the study area. Therefore, we accounted for potential large-scale spatial gradients in each CSI model by adding plots coordinates (i.e. of the centre point in the 2×2 km plots) as a smoother control covariate $s(X,Y)$, which allows for nonlinear spatial gradients. Hence, the model structure for the CSI was:

$$CSI_{j,p} = \text{year}_j + s(X, Y) + (1|\text{plot}_p).$$

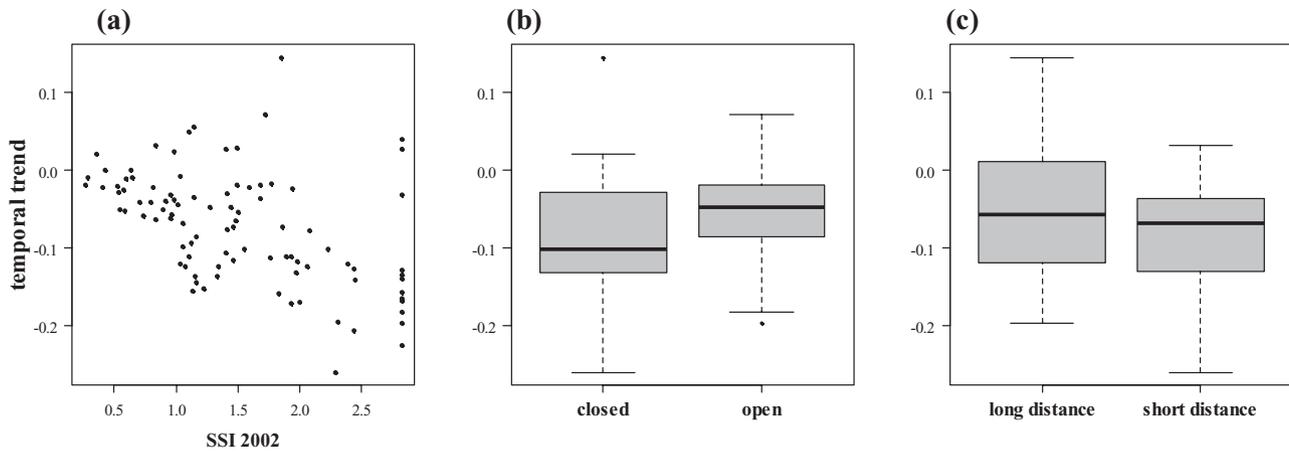


Figure 2 Impact of specialization in year 2002 (a), preferred habitat ('open' or 'closed', b), and migratory status ('long distance' or 'short distance', c) on the temporal trend of specialization of 94 species. For boxplots, the broad line, lower and upper bounds of each box correspond, respectively, to the median, 25% and 75% quartiles. Whiskers extend to the value distant to at most $1.5 \times$ the interquartile distance from the median. Black dots are values exceeding this distance.

Additionally, we visually examined the spatial autocorrelation in the residuals of our CSI models using the function 'correlogram' of the R package 'spatial' (Venables & Ripley, 2002). As no strong pattern of autocorrelation appeared in the residuals of our models (Appendix S5), we did not add any further spatial term to our models.

Analyses were conducted using the nlme (Pinheiro *et al.*, 2009), lme4 (Bates & Sarkar, 2008) and mgcv (Wood, 2006) packages of R 2.8.1 (R Development Core Team, 2008).

RESULTS

The slope of year effects for species-specific trends of the SSI over the period 2002–08 ranged from -0.26 (Hawfinch) to 0.15 (Orphean Warbler) (mean \pm SD = -0.07 ± 0.07) (detailed results in Appendix S6a). The across-species mean slope was not affected by the variability in the values of SSI_{02i} , suggesting that intra-annual stochastic variability of the SSI did not bias the trends (Appendix S4). Only 13 species showed null or non-significant positive trends in SSI, while 35 species showed significant ($P \leq 0.05$, $n = 27$) or near significant ($P \leq 0.1$, $n = 8$) negative trends. The 46 remaining species had non-significant negative trends.

The selected model for the trend in species SSI (Table 1) did not show any effect of year (estimate of year effect = 0.012 ± 0.017 , $t = 0.699$, $P = 0.49$). However, our model retained a negative interaction between years and SSI_{02i} (estimate = -0.055 ± 0.008 , $t = -6.73$, $P < 0.001$, Fig. 2a), suggesting that the SSI of more specialized species decreased more than that of generalists during the period (Fig. 3a). Random fluctuations of the SSI_{02i} did not affect this interaction (Appendix S4). The trend in SSI values also depended on the habitat category: species in open areas tended to generalize less rapidly than those preferring closed habitats [interaction year \times category, estimate (habitat open) = 0.0416 ± 0.012 , $t = 3.432$, $P < 0.001$, Fig. 2b]. Short-

distance migrants generalized faster than long-distance migrants [interaction year \times migratory status, estimate (short-distance migrants) = -0.0328 ± 0.012 , $t = -2.628$, $P < 0.01$, Fig. 2c].

The most specialized species in 2002 were also the least abundant (trend model, SSI_{02i} effect confidence interval = $[-2.671, -2.281]$). There was a significant positive trend in densities across years (trend model, year effect confidence interval = $[0.034, 0.196]$), weakly dependent on the initial specialization level ($SSI_{02i} \times$ year interaction confidence interval = $[0.0003, 0.0976]$); yet, a detailed analysis revealed that the significance of this interaction was exclusively due to the trend of a single rare and localized species (the Ortolan Bunting). Simple linear regressions showed that the SSI of 34 species (36%) were negatively related to $\log(\text{density})$ variations; 46 species had a negative but non-significant trend ($P > 0.1$) and only 14 species showed a positive relationship between $\log(\text{density})$ and SSI, one of which was significant (see Appendix S6b). Nineteen out of 94 species (20%) showed an opposite trend between years and density; 10 had a positive density effect and a negative year effect, 9 the contrary. In our M_{Density} model, yearly variations in SSI were negatively correlated to yearly variations in species mean density (Table 1, Fig. 3b; estimate of $\log(\text{density})$ effect = -0.16 ± 0.05 , $t = -3.025$, $P < 0.01$), with a significant variation among species (species \times density, $F_{1,561} = 6.436$, $P < 0.05$).

When the SSI was fixed, the CSI_{02} significantly decreased over 2002–08 (mixed effect linear model, year effect interval = -0.005 ± 0.001 , Fig. 4a). This effect was about 10 times stronger when the SSI was considered to be a variable trait (CSI_y , year effect interval = -0.048 ± 0.001 , Fig. 4b).

DISCUSSION

We showed a significant decrease in habitat specialization between 2002 and 2008 for 35 species out of 94. Despite high

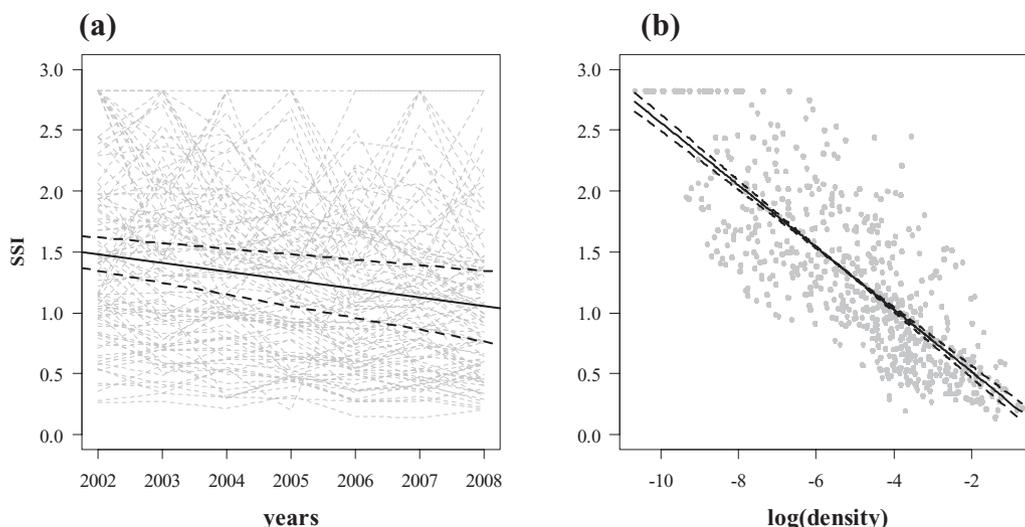


Figure 3 (a) Temporal trend in the Species Specialization Index (SSI) and (b) variation of the SSI respective to log-transformed density. Grey lines in (a) represent the variations of species SSI across the period. Each point in (b) corresponds to a species in a given year. Plain black lines and associated dashed black lines are the estimates of the linear models $SSI = f(\text{years})$ (a) and $SSI = f(\log(\text{density}))$ (b) ± 1.96 SE.

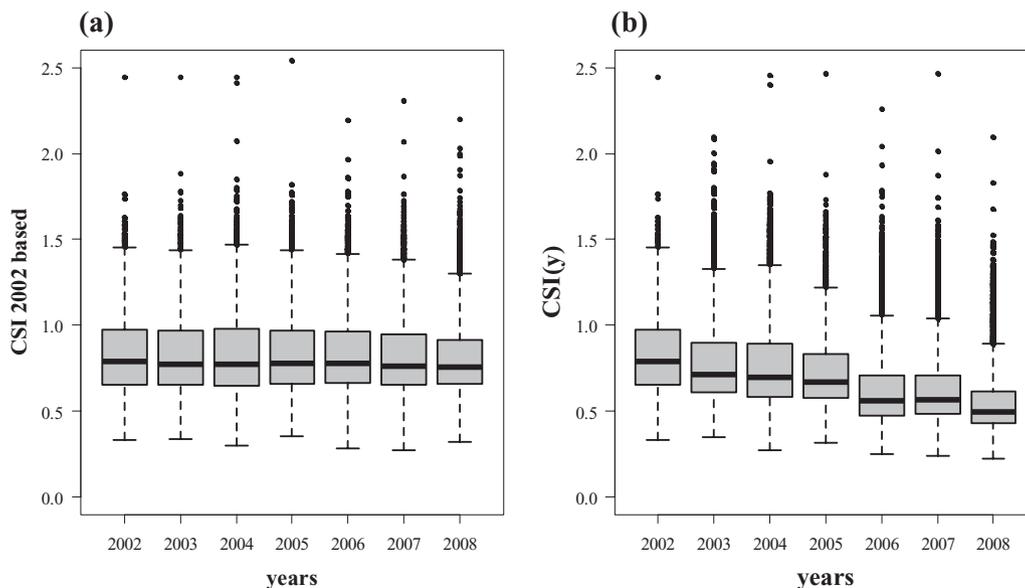


Figure 4 Temporal change in the Community Specialization Index (CSI) over the study period. In (a), the CSI is the mean specialization of species comprising the point level communities, weighted by species density, using the species specialization index for the year 2002 for all years, and thus only reflects variation in the composition of communities (CSI_{02} in the main text). In (b), the CSI is based on a specialization index recalculated each year for each species (CSI_y in the main text). It reflects not only changes in community composition, but also within species changes in specialization. The broad line, lower and upper bounds of each box correspond, respectively, to the median, 25% and 75% quartiles. Whiskers extend to the value distant to at most $1.5 \times$ the interquartile distance from the median. Black dots are values exceeding this distance.

between-species variability, the initially most specialized species (in 2002) generalized most in the following years, and this trend was not due to random variations in the SSI of each species (Appendix S4). We also found a weak but general increase in bird densities over this period. Specialization was related to density: generalist species displayed more abundant local popu-

lations than specialists. Species occurring at higher densities also tended to be more generalist over time. Note, however, that although correlated to density, our specialization index cannot be simply reduced to a nonlinear transformation of density. Indeed, two species with equal mean densities may have different standard deviations of densities across habitats.

Bird communities progressively became less specialized over time due to contrasted trends between specialist and generalist species (CSI₀₂ model) and to a simultaneous decrease in the specialization level of many specialized species (CSI_y model). Trends in the observed CSI at the point level could be affected by the increased efficiency of observers at points that they had previously surveyed (Kendall *et al.*, 1996); however, Jiguet (2009) showed that this effect only occurred between the first and second years. Moreover, to influence our conclusions, such a bias should be directed towards specialist species, which are most often rarer and less well known by volunteers. Hence, the consistent negative trend in CSI across 7 years is unlikely to be the result of this learning effect. Our results were neither biased by yearly variations in sample size or spatial distribution, nor by variations in species detectability (Appendix S5a, detectability, and S5b, number of points). We also ruled out potential bias due to undetected or unreported local habitat changes (Appendix S1c).

The tendency to generalize over a short time-scale (2002–08) more probably results from consistent change in species specialization rather than from environmental fluctuations. Habitat quality may have gradually changed over time at a landscape scale beyond any qualitative local habitat change. For instance, populations may be affected by increasing fragmentation of a given habitat without any change in the habitat itself. If the habitat of a given point and its surroundings is degraded, bird densities should decline in this point, forcing the SSI of the most specialized species to decline. In the meantime, habitat degradation could allow more generalized species to exploit habitats from which they were previously excluded, due to the relaxation of inter-specific competition with more specialized species. Therefore, our results document the temporal variations of realized specialization (Devictor *et al.*, 2010), and highlight the importance of accounting for the major sources of abundance variations when measuring specialization with field data.

Our results support the hypothesis that generalists tend to be more abundant and widely distributed than specialists (Brown, 1984; Gaston & Spicer, 2001). Additionally, we provide a seldom-addressed temporal dimension and an intra-specific approach to the link between specialization and density. Two questions remain to be explored in this respect: (1) how adaptive is the emigration of individuals in apparently non-optimal habitats, and (2) whether changes in the realized niche correspond to a plastic or a microevolutionary response of the species. If breeding performance is density dependent, the mean individual reproductive success in optimal habitats decreases as breeding density increases. Hence, the growth rate decreases as intra-specific competition rises, lowering the carrying capacity of the community up to a threshold above which breeding in suboptimal habitats (i.e. where densities are lower) becomes advantageous, leading to a decline in the across-habitat variance (Hanski, 1982; Dhondt *et al.*, 1994; Maurer & Taper, 2002). Behavioural responses could also occur if, for instance, species become less selective when occurring at high densities (Elkin & Reid, 2010). If optimal habitats remain unsaturated, or if carrying capacities vary with the exploitation of new habitats, the

threshold may never be reached (Hanski, 1982) and specialization may not vary or can even increase. This source–sink dynamic process may contribute to explaining our results: the 14 species which exhibited a null or slightly positive density effect on the SSI may not have reached such a threshold, while the 34 others may have overtaken this threshold and 46 may be nearing it. In this respect, accounting for data on reproductive success could add mechanistic support to our findings.

Interestingly, the SSI changed significantly more for specialists over time, supporting the idea that generalists exhibit fewer temporal variations in their apparent specialization level than specialists do, as they experience fewer among-habitat differences in breeding performance. Emigration of individuals in sink habitats may still be advantageous if they can recolonize source habitats when conditions become more favourable (e.g. if intra-specific competition in source habitats decreases). Such a mechanism could enhance species persistence in the landscape by maintaining more potential breeders.

Most species increased in density in suboptimal habitats, bringing into question the importance of intra-specific competition in the process of generalization. Additionally, 20% of the species exhibited opposite year and density effects, suggesting that density may not be the only driver of the changes in specialization. Indeed, although our best model retained a density effect, patterns of generalization may not be solely driven by changes in density. Migratory status and habitat preference were also retained, showing that variations in particular life-history traits (not necessarily linked to density) may play a significant role in species realized niche enlargement even over a short time period. Climate and landscape are among the most influential large-scale parameters influencing population processes or ecological niche (Stenseth *et al.*, 2002; Jackson *et al.*, 2009) and their long-term changes play a significant role in the homogenization of bird communities (Julliard *et al.*, 2004; Jiguet *et al.*, 2006, 2007). The effect of the migratory status could also reflect the fact that most migratory species are actually more specialized than sedentary species and thus generalize more rapidly, in accordance with the SSI₀₂ × year interaction. However, the same effect could appear if, under the effect of climate change, sedentary species advanced their phenology more in their preferred habitat than in others. In this case, the apparent generalization would only mirror a reduced detectability of sedentary species by the FBBS survey, which operates at roughly fixed dates. Yet, we believe this bias is unlikely as the trends in the SSI were close between short-distance and long-distance migrants. Further, given the phenology of our particular set of sedentary species, this bias would imply a phenology shift in preferred habitats exceeding 1–2 weeks in only 7 years.

The apparent niche changes related to species density may instead reflect either the accumulation of non-breeders in their optimum habitats or the definitive exclusion of the least competitive individuals from the source habitats, in high-density periods. Our results are based on a time lag which may not exceed four generations for most species (Cramp & Simmons, 1977); thus, although microevolution can occur rapidly in the

context of rapid environmental changes (Colles *et al.*, 2009), it seems more likely that the observed variations of specialization were related to plasticity. In the present study, we established a correlation – not a causal link – between yearly SSI and yearly species mean density; hence it cannot be decided whether the observed niche extension over such a short-term lag is a consequence or a cause of a density increase. Future comparison between breeding performances in various habitats in periods of low and high densities may help to disentangle adaptation from plasticity in the interaction between change in niche breadth and density.

Using a fixed specialization index per species (averaged over 2001–04), Devictor *et al.* (2008a) showed from FBBS data that the CSI decreased in a context of landscape degradation, due to the simultaneous negative trend of specialists and positive trend of generalists. Our results using SSI₀₂ as a reference are consistent with this pattern, even though the specialization index, sampling period and set of species were slightly different. Nevertheless, using a temporally variable SSI accentuated by a factor of 10 the negative temporal trend of the CSI previously observed using a fixed index. We found similar results using a CSI based on the presence–absence of species (i.e. without weighting by densities), showing that changes in community specialization are due to true changes in community composition and not only to variations in relative abundance (results not shown). Hence, the homogenization of bird communities due to more positive trends in generalists than in specialists is amplified by a negative trend in species-level specialization itself. Biotic homogenization in bird communities in France is therefore probably even stronger than reported by Devictor *et al.* (2008a).

Overall, our results raise questions about the causes, consequences and speed of short-term changes in species niche breadth. Addressing these issues could help us to assess the maximum acceptable scale and level of ecosystem change that permit it to maintain its functioning (Jackson *et al.*, 2009). Hence, taking short-term temporal variations of species specialization to various resources into account would be a significant improvement in a conservation perspective.

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SUPPORTING INFORMATION

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

Appendix S1 Information on bias linked to detectability, variations in the number of point counts in our data, variation in local habitat and sample size.

Appendix S2 Full list of the species considered, with summary information on their species specialization index (SSI), density values, migratory status and habitat traits.

Appendix S3 Detailed habitat classification and gradient of habitat opening.

Appendix S4 Summaries of simple regressions species specialization index (SSI)–year after resampling of the SSI for the year 2002.

Appendix S5 Spatial correlograms for the residuals of the community specialization index (CSI) models.

Appendix S6 Summaries of simple regressions species specialization index (SSI)–year and SSI–log(density) for each species.

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BIOSKETCH

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