LETTER

Spatial segregation of specialists and generalists in bird communities

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Abstract

Each species generally has a close relationship with one or more habitats and can therefore be classified as either specialist or generalist. We studied whether specialist and generalist species are spatially distributed independently of each other. Repeating the analysis for 100 of the most frequent terrestrial bird species recorded over the 10 000 sampled sites of the French Breeding Bird survey, we found that specialists were more abundant if the rest of the community was specialized, and that the inverse was also true. This pattern was far subtler than just a simple dichotomy: most species actually presented a maximum abundance at a value of community specialization similar to their own level of specialization. Bird communities appear very well defined along a specialist–generalist gradient. We believe this pattern becomes more apparent with habitat degradation. The consequences on both ecological services and community resilience may well be considerable.

Keywords

Abundance, competition, functional homogenization, GAM modelling, interaction milieu, niche theory.

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INTRODUCTION

Ordering species along a generalist/specialist gradient, or in other words, separating species with large ecological niches from those with smaller niches, is both practical and the subject of many theoretical issues. Indeed, the determinants and consequences of niche breadth have been the focus of numerous studies (review in Futuyma & Moreno 1988; Kassen 2002). Ecological theory states that niche-breadth differences among species are the result of an evolutionary trade-off between the ability of species to exploit a range of resources and their capability to use each one (the 'jack-of-all-trades is master of none' hypothesis; McArthur 1972; see also Levins 1962, 1968; Futuyma & Moreno 1988; van Tienderen 1991; Kawecki 1994). Such a trade-off has been associated with several life-history traits: specialist species are supposed to have lower dispersal abilities (Tripet *et al.* 2002; Brouat *et al.* 2004), are more strongly regulated by intra-specific competition (Dall & Cuthill 1997), and are less able to cope with environmental stochasticity (Sol *et al.* 2002) than generalist species. Hence, the way community functions is very likely to be influenced by the relative amount of specialist and generalist species. Despite this,

very little is known about the actual distribution of specialists and generalists in any given space.

Studying the spatial segregation of species according to their niche breadth would normally be addressed by studying spatial organization using, e.g. multivariate analysis, and trying to interpret observed associations according to the degree of specialization of the different species. We have developed an approach that we believe will be more efficient. The basic principle is to study how the abundance of a given species is predicted by the average characteristic of the rest of the community. We quantified the specialization of each species, and calculated (for each species and each study site) the average specialization of other species present at that site. We then studied whether abundance of a given species varied according to average community specialization and whether this trend differed between generalists and specialists. A large-scale data set from the French breeding bird survey was used to explore this question. We studied the spatial variation in abundance over more than 10 000 sampling points for the 100 most common terrestrial bird species in relation to the average specialization of the rest of the community. We paid particular attention to the type of relationship between

species abundance and community specialization. Our results suggest that bird communities are very well defined along a specialist–generalist gradient.

MATERIALS AND METHODS

Data source

Data came from the new Breeding Bird Survey scheme launched in France in spring 2001 (Julliard & Jiguet 2002). Observers were volunteer, skilled ornithologists, who were able to identify most common breeding birds from their song or through visual contact. Birds were counted on fixed plots during 5-min intervals, twice a year (both before and after the 8th of May), with 4–6 weeks between counts. For each species and each year, the maximum value of the two counts was retained. Each observer was asked to evenly distribute 10 such point-counts, carried out the same morning within a 2 by 2 km square plot. Each surveyed square was randomly selected within 10 km of the observer's house (or any location chosen by him or her). Such random selection (*c.* one of 80 possible squares) ensures that widespread habitats such as intensive farmland, ordinary forest, suburbs and cities, were surveyed. Previous analyses have shown that on a national level, the distribution of surveyed habitats closely matched the actual distribution of those habitats (Julliard & Jiguet 2002). Observers were asked to describe land use/habitat within 100 m of each point. A standardized, four-level land-use description was used, based on a similar tool developed by the British Trust for Ornithology (Crick 1992). In this paper, we used the first two levels of description, grouping categories to ensure a minimum coverage (Table 1). All squares surveyed at least once between 2001 and 2004 were considered ($n = 1022$, i.e. 10 220 point counts). Yearly counts were averaged for squares that were monitored over several years. We assumed that, for a given species, detection probability did not vary widely across habitats. Hence, counts were assumed to be proportional to density. Given the widespread distribution of observers, France is well covered by the scheme.

Species that only breed in wetlands (e.g. herons, gulls, waders, reed-bed passerines, etc.), were excluded from the analysis because they are not suitably monitored by the scheme. In this paper, we considered the 100 most detected (i.e. most frequent in the database) terrestrial bird species. This represents slightly more than 50% of the species but 99% of the counted individuals (excluding water birds). All species considered were detected at least 200 times (the total for the 100 selected species is 565 251 counted individuals). According to the French breeding bird Atlas (Yeatman-Berthelot & Jarry 1995), most of these species are widely distributed (96 species are found in more than 25% of the 1091 grid cells covering France, the remaining four are typical Mediterranean species).

Table 1 Habitat categories, and their distribution (number of surveyed points) in the three main biogeographical zones. Habitat categories were pooled so that each category was covered by at least 30 point counts per biogeographical area. The few data points located in the alpine zone were relocated to the nearest of the three main zones.

Land use/habitat categories	Biogeographical zone		
	Atlantic	Continental	Mediterranean
Deciduous woodland	579	525	95
Coniferous woodland	73	115	82
Mixed woodland	178	211	129
Young forest (< 5 m)	40	30	36
Heath, scrub	84	43	204
Coppice	71	53	34
Dry natural meadow	49	40	117
Moorland	35	50	55
Marshland	191	65	38
Ploughed meadow	373	248	42
Unploughed meadow	426	625	49
Mixed farmland	796	437	57
Openfield	1034	455	74
Permanent crop	164	63	256
Urban settlement	293	104	30
Suburban settlement	198	124	66
Rural settlement	386	277	71
Near open water	185	125	38

Species specialization index

Ideally, specialization should be measured as the breadth of the species' ecological niche considering all its dimensions. In practice, the quantification of specialization often depends on the type of species considered (e.g. diversity of host plants in butterflies; Warren *et al.* 2001; tongue length in bumblebees; Goulson *et al.* 2004). A more general way of quantifying specialization is to count the number of habitat classes in which a given species is known to be present. This measure allows the ordering of species from specialists (occurring in few habitat classes) to generalists (occurring in many habitat classes). Yet, such an approach usually depends on expert knowledge (an ability to determine which habitat is appropriate for which species; e.g. Gregory *et al.* 2005) and ignores potentially large variations in density among habitat classes. Indeed, two species could be considered as generalist according to presence–absence data even if one is present in 10 habitats with similar densities among classes, and the other is also present in 10 habitats but in varying densities (source–sink dynamic may cause such pattern; Pulliam 2000). Therefore, to account for density variation across habitat, we quantified the degree of habitat specialization as the variance of average densities among the 18 habitat classes considered (Fig. 1a). To
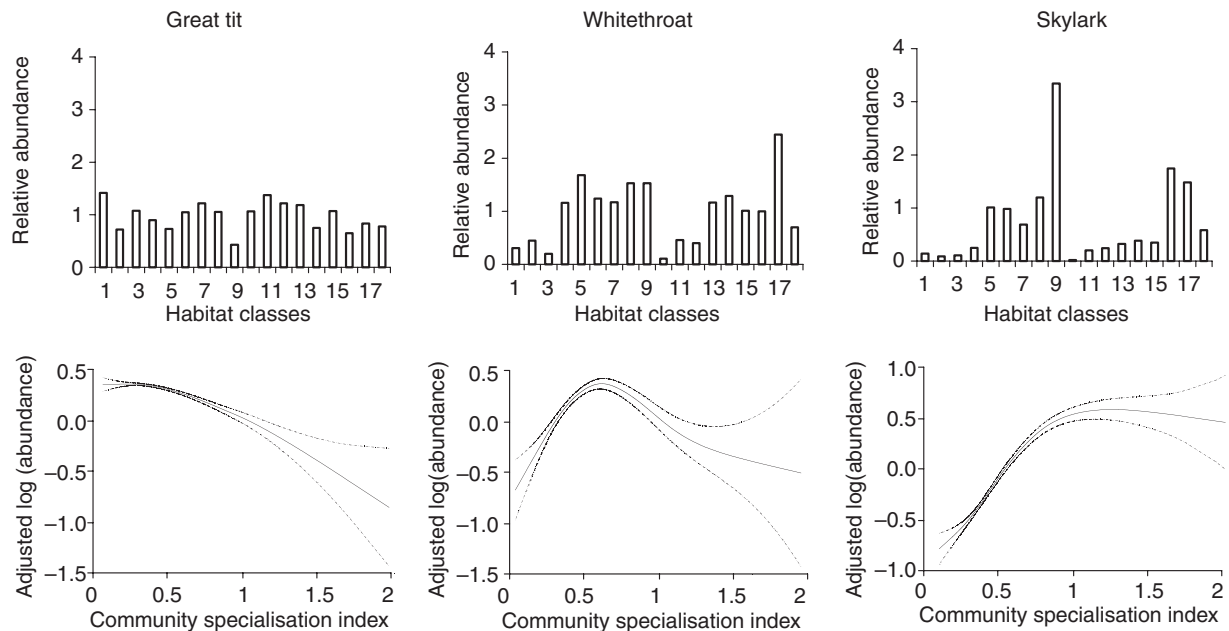
Figure 1 (a) Relative abundance (abundance/mean) variation among the 18 habitat classes for three species. Habitats are ranked as in Table 1. Left, the great tit, *Parus major* L., a generalist species (species specialization index, SSI = 0.29; mean abundance: 0.73 individuals per point count); centre: the whitethroat, *Sylvia communis* L., an intermediate species (SSI = 0.65; mean abundance: 0.23 individuals per point count); right, the skylark *Alauda arvensis* L., a specialist species (SSI = 1.16; mean abundance: 0.61 individuals per point count). (b) The relationship between abundance of the same three species and specialization of the rest of the community (CSI). Fit from a non-parametric spline function with 4 d.f., adjusted to habitat classes and using a log link and a Poisson error; dotted line shows ±1 SE.

obtain a metric statistically independent of the average species density, we chose the coefficient of variation (standard deviation/average) as a measure of each species specialization index (SSI).

Interestingly, one could also calculate SSI from the number of occupied habitat classes. Assuming equal densities in occupied habitat and null density in others, SSI for a species present in h habitat classes among H possible habitat classes is

$$SSI = \left(\frac{H}{h} - 1\right)^{1/2}.$$

Conversely, SSI may be converted into an equivalent proportion of occupied habitat classes:

$$\frac{h}{H} = \frac{1}{(SSI^2 + 1)}.$$

For example, SSI = 1 corresponds to a species that is present in half of the habitat classes. Hence SSI is closely related to number of occupied habitat classes but does not rely on expert knowledge to decide which habitat is occupied and which is not, and takes into account variation in density among occupied habitats. Among the 100 selected species, SSI ranged from 0.23 (equivalent to present in ≈ 17 of 18 habitat classes) for the blackbird (*Turdus merula* L.) to 2.23

(equivalent to present in ≈3 of 18 habitat classes) for the lapwing (*V. vanellus* L.).

Such a measure of specialization may be biased if the density of species and habitat class distribution co-vary spatially (e.g. geographical cline). For example, a generalist species more abundant in the Mediterranean region, will appear more specialized than it actually is on a nationwide scale, because it is relatively more frequent in habitat classes that are over-represented in the Mediterranean and relatively less frequent in habitat classes that are under-represented in the Mediterranean. To overcome this problem, we calculated specialization indices for each species in France's three main biogeographical zones (http://dataservice.eea.eu.int/dataservice/metadetails.asp?id=308). A national specialization index was then calculated as the average of the zone-specific specialization indices, weighted by the proportion of the species population found in each zone. The latter was calculated from the average density per point in each zone and the surface area of the different zones. In Appendix 1, we explored how robust SSI is when applied to a small sample size.

Analysis

The aim of the analysis was to study the relationship between the abundance of a species and the degree of

specialization of the bird community. The community specialization index (CSI) was calculated from the average SSI of the individuals counted in that community (i.e. that point count; on average 18 of the 100 species are detected at a given site). In order to avoid dependency between the different variables, we calculated the CSI for each species and for each point (excluding the particular species considered). Then, the variation in abundance of each species (including 0 counts) was modelled using log-linear Poisson regression, the standard for data based on counted individuals (Gregory *et al.* 2005). For most species, few individuals were counted during the 5 min of observation and, within habitat classes, the distribution of counts does not depart from a Poisson distribution (Julliard *et al.* 2004). However, some species may be seen in groups. This causes a departure from the hypothesis of independence between individual detection probability, and could lead to heterogeneity in the data set. To reduce the problem, all counts were levelled to a maximum value of 10.

All considered species show some habitat preference. Clearly, what causes variation in abundance within a species' preferred habitat is likely to differ from that which causes the variation in non-preferred habitat. For example, the causes of skylark (*Alauda arvensis* L.) abundance variation in farmland are certainly different from those for woodland, and the latter is much less meaningful. Hence, for each species, we selected the nine (of 18) densest habitat classes. Despite this selection, even the most generalist species of our data set were likely to exhibit systematic variation in abundance among the different selected habitat classes. We included habitat classes as well as biogeographical zones as explanatory variables in all models of abundance spatial variation. The equation of the model was therefore:

$$E(\text{abundance\_species}_i) = \text{factor(habitat)}$$
$$+ \text{factor(biogeographic\_zone)} + f(\text{CSI})$$

where $f(\text{CSI})$ is a function (see below) of CSI. Hence, only within-habitat classes variation in abundance was modelled as a function of CSI. In the case of over-dispersion (residual deviance > residual d.f.), deviance was divided by an inflation factor (residual deviance)/(residual d.f.).

We paid particular attention to the shape of the relationship between abundance and CSI. We systematically fitted four models with increasing complexity: (i) no effect of CSI, (ii) linear effect, (iii) linear + quadratic effect, and (iv) nonlinear effect fitted using general additive model (GAM) and the default spline function with 4 d.f. [noted s(CSI)]. The latter model gives an estimation of the maximum deviance that could be explained with a parametric function with 4 d.f. In order to assess whether the linear and quadratic models were adequately modelling the shape of the relationship between abundance and CSI, we

compared the quantity of deviance explained by these models with the quantity of deviance explained by s(CSI). Given that the linear effect is estimated with 1 d.f., and s(CSI) with 4 d.f., we expected that, by chance only, the linear effect would explain 25% of the deviance explained with s(CSI). Similarly, we expected that the addition of a quadratic effect to a linear effect would explain (by chance only) one-third of the remaining deviance explained by s(CSI) after accounting for the linear effect. Basic statistics on proportions of deviance explained (average and standard error) are calculated after logit transformation, but for clarity, the outcomes are expressed as percentage.

The quadratic model implies that abundance presents an extremum (maximum or minimum) value for a particular value of CSI. Such a value (CSI_{max}) can be estimated from the parameter estimates of the model. If the estimates for a quadratic model are:

$$E(\text{Abundance}) = a_0 + a_1 \text{CSI} + a_2 \text{CSI}^2$$

then the extremum abundance is obtained for

$$\text{CSI}_{\text{max}} = -\frac{a_1}{2a_2}.$$

The associated variance may be estimated from the variance and covariance of a_1 and a_2 as follows (Ashton 1972):

$$\text{Var}(\text{CSI}_{\text{max}})$$
$$= \left(-\frac{a_1}{2a_2}\right)^2 \left[\frac{\text{Var}(a_1)}{a_1^2} + \frac{\text{Var}(a_2)}{a_2^2} - \frac{2\text{Cov}(a_1, a_2)}{a_1 a_2}\right].$$

RESULTS

For most species, abundance was strongly correlated to the CSI (Fig. 1b). An important question is whether we had enough data to detect a relationship for the less abundant species. As expected for a biologically significant effect, the statistical significance of the effect was partly related to sample size [correlation log(explained deviance), log(sample size); $r^2 = 0.40$]. However, even among the less extensively monitored species, the test could be highly significant (range χ^2, d.f. = 4, of s(CSI) among the 10 less abundant species: 7.51–89.99), suggesting a good ability to detect existing relationships.

For 80 of the 100 species, the linear effect of CSI was statistically significant ($P < 0.05$), most of them with a very low associated *P*-value (average effect of CSI: χ^2, d.f. = 1: 91.71, SD = 151.70). The coefficient of the slope relating species abundance to the specialization index of the rest of the community was strongly correlated to the SSI (Fig. 2a). The generalist species have a negative slope, indicating that their abundance is higher in the less specialized communities and lower in the more specialized. The inverse is also true
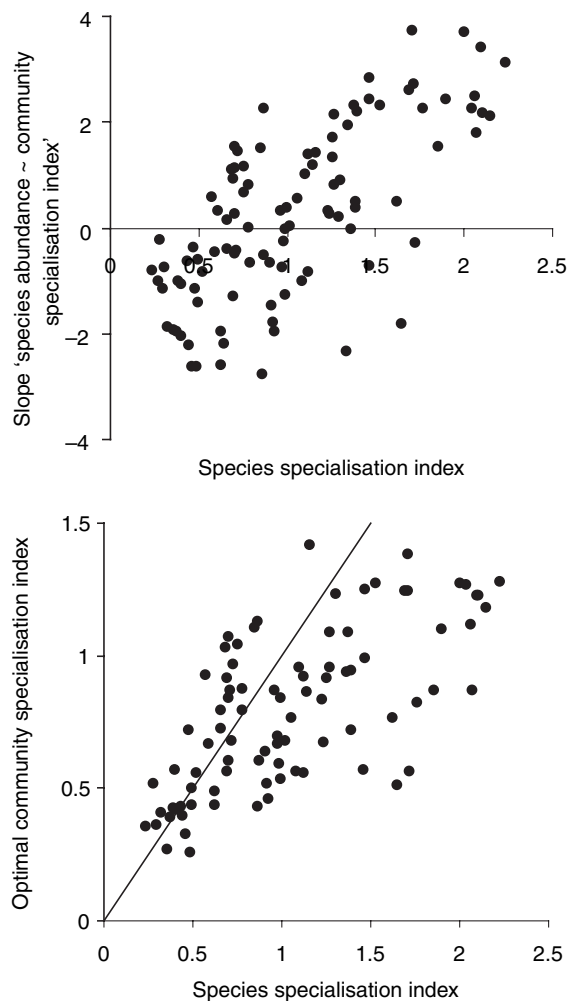
Figure 2 The distribution of specialist and generalist species in specialized and unspecialized community. (a) For each species, a linear model relating species abundance to average specialization of the rest of the community (CSI) was fitted. Generalist species tend to have a negative slope (abundance decreases with increasing CSI) while specialist species tend to have a positive slope (abundance increases with increasing CSI) ($r^2 = 47\%$; $n = 100$; $P < 0.0001$). (b) For each species, a quadratic model relating species abundance to CSI was fitted. For 87 of them, the model predicts an accurate value of CSI for which species abundance reaches an optimum (CSI_{max}) value. This value was close to the species' own specialization index (the line is for equal CSI_{max} and species specialization index) ($r^2 = 46\%$; $n = 87$; $P < 0.0001$).

for specialized species. We then systematically modelled abundance as a function of $CSI + CSI^2$. The results were extraordinarily consistent among species: 96% of species presented a positive coefficient for the linear effect and a negative coefficient for the quadratic effect, that is, evidence that abundance presented a maximum (and not a minimum) for a particular positive value of CSI. Among the four exceptions, one exhibited little relationship at all with CSI

Table 2 Assessing the fit of the relationship between abundance and CSI. The deviance explained by each model was compared with the deviance explained by the non-parametric spline function s(CSI). For a given model, the expected amount of deviance explained was calculated from the number of d.f. and deviance not yet accounted for by the immediate simplest model (see Materials and methods for more details). Figures are an average proportion ±1 SE of the deviance accounted for by each model, for the 100 species considered. Note that averages were calculated after logit transformation.

	CSI	$CSI + CSI^2$	$CSI + CSI^2 + CSI^3$
% of s(CSI) deviance actually explained	36.0 ± 5.4	91.5 ± 1.1	96.6 ± 0.5
Expected % of s(CSI) deviance explained by chance only	25.0 ± 0.0	66.9 ± 2.0	96.0 ± 0.5

(deviance explained by s(CSI): 2.49; i.e. the smallest value), one had both a negative slope for the quadratic and the linear term, that is a predicted optimum for a negative value of CSI. It was only the remaining two that presented a pattern which was opposite to most others, having a negative slope for the linear effect and a positive slope for the quadratic effect.

In order to assess the fit of the linear and quadratic model, we compared the amount of deviance explained by these models to the amount of deviance explained by the non-parametric spline function s(CSI) (Table 2). The proportion of explained variance was compared with the expected proportion of variance explained by chance alone (see Materials and methods). The linear model accounted for $36 \pm 5\%$ of the deviance explained by s(SSI), slightly higher than the expected 25%. The quadratic model accounted for a noticeably high $91 \pm 1\%$, considerably larger than the expected $67 \pm 2\%$. As a further check, we added a cubic effect to the quadratic model. The cubic model accounted for 96.6 ± 0.5 of the explained variance by s(CSI) not differing from the 96.0 ± 0.5 expected by chance alone. Ultimately, we concluded that the relationship between the abundance of a species and CSI is better explained by a quadratic model than by a linear term only, but that there is no evidence that the relationship is more complex than quadratic.

As mentioned, for all species but four, the quadratic model predicted a positive maximum abundance (CSI_{max}). For some of them, CSI_{max} had a large standard error, in particular when the quadratic term was close to 0 (in which case the predicted relationship is almost linear for the observed range of CSI). We considered that CSI_{max} was correctly estimated if the standard error was smaller than the observed standard deviation of CSI in the data set (0.19). This excluded 13 species, including the four species not

presenting a meaningful value of CSI_{max}, which all had a large standard error. The average standard error of CSI_{max} for the remaining 87 species was 0.06. For these species, there was a strong positive correlation between CSI_{max} and the SSI (Fig. 2b). Examining the figure further revealed that for most species (except some of the most specialized ones), CSI_{max} was even close to their own specialization index. Hence, species tend to reach their maximum abundance in sites where the average specialization index of other species tends to be similar to their own: generalist species prefer less specialized communities, specialist species prefer more specialized communities, and intermediate species prefer moderately specialized communities.

DISCUSSION

We quantified the specialization of bird species as the variance of their density among habitat classes. We then characterized species assemblage in a particular site as the average specialization of individuals present at that site. We found that most bird species tended to reach maximum abundance in bird assemblages that presented a CSI close to their own.

Methodological considerations

We first want to emphasize that the results we found are not mere artefacts due to the way SSI and CSI) were calculated: (i) for a given species and a given site, CSI was calculated excluding individuals from that species. Hence, SSI of a given species was not used when estimating the slope between abundance and CSI, or when estimating CSI_{max}, for that species; (ii) SSI were calculated only from *among* habitat classes variation in abundance, while the relationship between species abundance and CSI was modelled with habitat classes taken into account, that is using only *within* habitat classes variation in abundance; (iii) CSI is not a direct function of species abundance but rather measures the proportion of specialists and generalists in the community.

We quantified specialization as the distribution of abundance among habitat classes. Both in ecological and evolutionary studies, specialization is often defined using narrower ecological traits such as diet breadth. Granted, specialization quantified according to the methods we used only partly correlates with specialization defined using a specific ecological trait. For example, species with a specialized diet are likely to frequent only a few habitat classes, but some species that frequent few habitats may actually have a large diet breadth. In other words, habitat specialization is likely to integrate specialization over a wide variety of traits, but does not supply information on the detailed biology of specialization. On the other hand, such a crude way of calculating specialization allows the application

of this method to virtually any organism for which variation in abundance may be estimated over a range of habitat classes. The method proved to be robust even with fairly small numbers (see Appendix 1). However, for very rare or localized species, using number of occupied habitat classes rather than variation in density may be a more robust method. Fortunately, specialization may be calculated with one or another source of data interchangeably (see Materials and methods).

Community specialization index was calculated as the average SSI of all species (but one) found somewhere, weighted by the number of individuals counted. Strictly speaking, the 100 species considered do not form a meaningful ecological community, as their only common property is to breed in France, and the subset found on a given site is likely to include insectivores, seed-eaters, raptors, migrants, sedentary species, ground-dwellers, aerial-feeders, etc., i.e. a mixture of species with very different ecology. We do not believe that a given species is actually interacting with all the other species present in that place. Rather, the underlying hypothesis is that the relative amount of generalist or specialist species at a given site is meaningful with respect to the biological characteristic of that site. Because specialization is quantified with the same method for all species, it is legitimate to average SSI of very different species.

Biological considerations

We found that the average specialization of the different species within a community tended to vary spatially, and that most species reached a maximum abundance in sites carrying a species assemblage with an average specialization index similar to their own. Taken together, these results indicate that species with a similar specialization index tend to aggregate. Such a pattern was not only highly significant, but explained a surprisingly large quantity of the observed variation. *R*-squares in Fig. 1 reach 46% and 47%, which is rather unusual in ecological studies (Møller & Jennions 2002).

We believe we found such evidence for a strong structure because of the rather unorthodox way we analysed bird assemblage: (i) we focused on species' abundance rather than on species' presence–absence. This is a more powerful method for detecting patterns, and (ii), more importantly, we did not attempt to associate species together but rather, we correlated species' abundance to an average biological trait for the rest of the community. Interestingly, this approach fits well with the recent recommendations by McGill *et al.* (2006) which consist of reconsidering community ecology using functional traits (rather than species identity) and in characterizing biotic interaction through a quantitative description of the rest of biodiversity (rather than consid-

ering a species list), a so-called 'interaction milieu'. We intentionally chose a trait quantifying species' habitat specialization. The concept of specialization is at the heart of niche evolution theory (Futuyma & Moreno 1988), and a central concern in understanding community organization (e.g. Chesson 2000; Gravel *et al.* 2006). Nevertheless, we discovered a pattern from which it is currently difficult to infer process, i.e. the mechanisms leading to such a structure (such as inter-specific competition) have yet to be explored.

Theory predicts that specialization is an expected evolutionarily response to habitat stability (in space or time), and conversely, that generalist strategy is a response to the lack of stability of the environment (Futuyma & Moreno 1988; Wilson & Yoshimura 1994). The pattern we observed may therefore have something to do with the current level of habitat perturbation. We found that within a given habitat category, generalist species tend to aggregate at some sites and specialist species tend to aggregate at others. A possible explanation for such a pattern is that specialists prefer the most stable sites and generalists the more unstable ones. Perhaps the most curious result is that intermediate species prefer intermediate situation rather than one or other of the extremes. Such habitat perturbation may be natural or linked to human activities. Indeed, specialized species of various groups have been found declining throughout the world (plants, Fischer & Stöcklin 1997; Rooney *et al.* 2004; butterflies, Warren *et al.* 2001; carabid beetles, Kotze & Ohara 2003; bumblebees, Goulson *et al.* 2004; coral reef fish, Munday 2004; birds, Julliard *et al.* 2004; marsupials, Fisher *et al.* 2003). This poor success rate for specialists, with communities increasingly comprised of generalists, is part of the global process of biotic homogenization (McKinney & Lockwood 1999; Olden *et al.* 2004), a consistent signature of the consequences of global changes on animal and plant communities. One may hypothesize that the pattern we have discovered is linked to the global alteration of ecosystems: generalist species may have a high success rate in degraded habitats, possibly as a result of the relaxed competition from specialist species who have been badly affected by the degradation.

CONCLUSION

We have shown a strong pattern of spatial organization in bird species assemblages, with local assemblages consisting of a subset of species having similar degrees of specialization. Such a strong pattern contrasts with previous studies which have generally been inconclusive in determining which ecological attributes determine variation in abundance across species (e.g. Hubbell 2001). The reasons behind the success of our approach warrants further consideration. An important question emerges: do ecosystems, which support communities consisting either of specialists or of generalists,

function in the same way? Several systematic differences in life-history traits between specialists and generalists have been predicted. For example, specialists are supposed to have poor dispersal ability compared with generalists (Tripet *et al.* 2002; Brouat *et al.* 2004). This could have consequences on the spatial dynamic of specialized vs. generalist communities. Finally, specialists within a given habitat should have a long history of co-evolution, while generalist communities are possibly a recent consequence of global change. Hence, specialists within a specialized community are likely to show ecological completeness while generalists in a generalist community are likely to be ecologically redundant (Olden *et al.* 2004). Altogether, this may have wide implications on the ecological services and on the long-term resilience of these communities (Loreau 2000).

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APPENDIX 1 SSI AND SMALL SAMPLE SIZE

Another problem specific to our data set may occur because densities are estimated from counted individuals. If few individuals have been counted, density in each habitat class will be estimated with low precision. As SSI is calculated from a variance, this will not only cause imprecision but also will positively bias the index. To estimate the importance of such a bias, we calculated the SSI of a perfectly generalist species (equal densities in all habitat classes; expected SSI is 0), for which habitat-specific densities were estimated from a finite number of individuals randomly distributed among 10 220 potential points, themselves distributed into 18 habitat classes to the same proportion as in Table 1. We found that the bias of the estimated SSI was a linear function of the inverse of the squared-root of the number of counted individuals N ($SSI = 4.51N^{-0.5}$). We thus calculated the expected bias for each of the 100 species, according to the number of individuals actually counted: it ranges from +0.024 to +0.310 from the most abundant to the least abundant of the species considered. The raw specialization index calculated from the data appeared far more variable (from 0.234 to 2.228). A corrected specialization index was estimated as the raw index minus the expected bias. The relation between the raw and corrected specialization index was very strong ($r^2 = 0.98$, $n = 100$), i.e. only 2% of the variation in SSI among species is attributable to biases from sample size. We thus concluded that overestimating SSI of poorer sampled species was not important in our data set and was therefore neglected.