Research

Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation

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In this paper, we tested whether the spatial distribution of a given species in more or less fragmented and disturbed landscapes depends on the species habitat specialization. We studied 891 spatial replicates from the French Breeding Bird Survey (FBBS) monitored at least two years during 2001–2005, and two independent landscape databases measuring respectively landscape fragmentation and recent landscape disturbance on each FBBS replicate. We used a continuous habitat specialization index for the 105 most common bird species monitored by the FBBS. We further modelled the spatial variation in abundance of each species according to fragmentation and disturbance across FBBS replicates, accounting for habitat differences and spatial trends. We then tested whether more or less specialized species responded to landscape fragmentation and disturbance. We found that the more specialist a species, the more negative its spatial response to landscape fragmentation and disturbance. Although there was a very high variation around these tendencies indicating that there are many other drivers of species distribution, our results suggest that measuring specialization may be helpful in predicting which species are likely to thrive in human degraded landscapes. We also emphasize the need to consider both positive and negative species responses when assessing consequences of habitat change in communities.

Global biodiversity loss is not occurring at random. Human-induced environmental changes act as a non-random filter, selecting from a potential pool for those species best able to survive within modified ecosystems (Smart et al. 2006). Beyond numerous decreasing species (the losers), there are also many increasing species (the winners) (McKinney and Lockwood 1999). The growing recognition that species are not equally at risk when facing global changes is remarkably highlighted by the recent increase in studies focusing on biotic homogenization (Olden 2006a). Biotic homogenization refers to the process by which the genetic, taxonomic or functional similarity of two or more species assemblage increases over space and/or time (Olden 2006b). This process typically occurs if some species, sharing a given trait, tend to replace other species, sharing many different traits.

Biotic homogenization is generally quantified as the increase in the pairwise community similarity between two sites (and/or time periods) through similarity index (e.g. Jaccard; Bray-Curtis index) calculated with records of species presence/absence between sites (and/or time periods). However, this approach does not embody the identity of species and is weakened because change of community similarity is scale dependent and not always clearly linked with a change in ecosystem integrity (Rooney et al. 2007).

To refine the question of which species should win or lose in the current biodiversity crisis, the use of the specialist–generalist concept should be useful. Indeed, natural selection induces more or less specialized strategies among species by presenting an evolutionary tradeoff between specializing to perform a few activities well, and generalizing to perform many activities fairly (Levins 1968). Ecological specialists are expected to benefit from environments that are relatively homogeneous (in space and/or time) whereas ecological generalists should benefit from environments that are heterogeneous (in space and/or time) (Futuyma and Moreno 1988, Kassen 2002, Marvier et al. 2004, Östergård and Ehrlén 2005). The fact that habitat degradation should negatively affect specialists is predicted by niche evolution theory.

Empirically, emerging evidence suggests that specialist species across taxa are declining throughout the world (plants, Fischer and Stöcklin 1997, Rooney et al. 2004; butterflies, Warren et al. 2001; carabid beetles, Kotze and O'Hara 2003; bumblebees, Goulson et al. 2005; coral reef fish, Munday 2004; birds, Julliard et al. 2004; marsupials, Fisher et al. 2003). This poor success of specialist species should result in functionally homogenized communities (Olden 2006a). Yet, this symptom of biodiversity loss was only described or correlated to static environmental variables at particular sites (Jonsen and Fahrig 1997), but hardly linked with explicit large-scale human driving forces (but see Devictor et al. 2007a, 2007b). Therefore, the question of how more or less specialized species respond to land-use change is still hypothetical.

In this paper, we address the question of how densities of more or less specialized bird species respond to the fragmentation and the temporal disturbance of the landscape. We address this question using 891 2×2 km replicates monitored at least two years by the French Breeding Bird Survey during 2001–2005. We used two independent landscape surveys to quantify for each site, landscape fragmentation and landscape disturbance, respectively. We tested, for the 105 most common terrestrial bird species, whether more or less specialized species were equally distributed along fragmentation and disturbance gradients.

Material and methods

Bird data collection

The French Breeding Bird Survey (FBBS) is a standardized monitoring program in which 80 skilled volunteer ornithologists identify breeding birds by song or visual contact each spring (Julliard and Jiguet 2002). Each observer provided a locality, and a 2×2 km plot to be prospected was randomly selected within a 10 km-radius of this location (i.e. among 80 possible plots). Such random selection ensured the survey of varied habitats (including farmland, forest, suburbs and cities) (Fig. 1). We selected each plot monitored at least two years during 2001–2005 (n = 891). For a given year, each selected plot was monitored in two annual visits during spring, one before and one after 8 May, with 4–6 weeks between the two visits.

In each plot, the observer carries out 10 evenly distributed point counts, within which all individuals are recorded during a five minutes period. Point counts are at least 300 m apart and sampled in the same order on each occasion. To be validated, the count must be repeated on
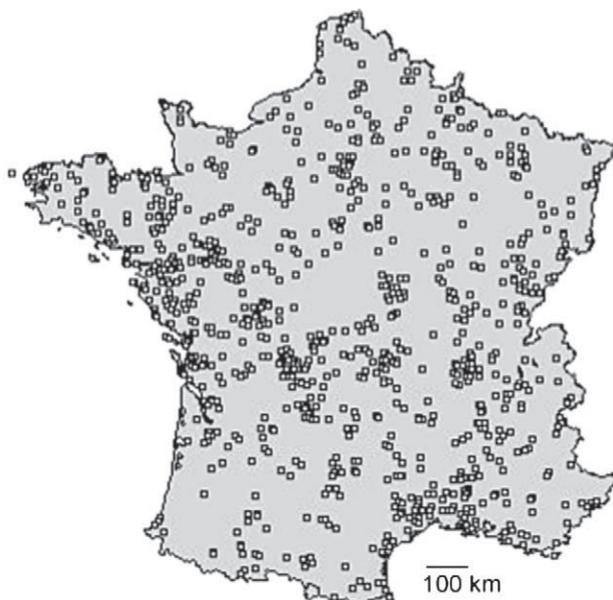

Fig. 1. Spatial distribution of the French Breeding Bird Survey plots. Each square (n = 891), is a 2×2 km landscape sampling replicate in which 10 point counts, evenly distributed in the square were monitored at least 2 years between 2001 and 2005.

approximately the same date each year (± 7 days from April to mid June) as well as the same time of day (± 15 min within 1–4 h after sunrise). For a given point count, the maximum count of the two annual visits was retained and then averaged over five years (2001 to 2005). We excluded from the analysis species that only breed in wetlands (such as herons and gulls) because they are not appropriately monitored by this scheme.

For each point count, the surroundings within a fixed 100 m radius were classified by observers as belonging to one habitat among a standardized habitats list. This list was organized into a hierarchical standardized 4-levels land use description, adapted from the one developed by the British Trust for Ornithology (Crick 1992). The first level was a coarse division into four main habitat categories: farmland, natural, urban and a last class comprising all other types of habitat, such as wetlands and bare rocks. These main habitat categories were then subdivided into a second level classification of 18 habitat classes, grouping categories to ensure a minimum coverage (deciduous woodland, coniferous woodland, mixed woodland, young forest, scrub, coppice, dry natural meadow, moorland, marshland, ploughed meadow, unploughed meadow, mixed farmland, openfield, permanent crop, urban settlement, suburban settlement, rural settlement, near open water). In this paper, we used this second level of description as a qualitative description of the point-count habitat.

Measuring species specialization

The measure of a given species' specialization for any resource may be described as the position and shape of that species' response in abundance to the resource gradient (Austin et al. 1990). We assume that a given species is therefore more specialized to certain habitat classes if its density there is higher than elsewhere. Conversely, a species which density varies little across habitats can be considered as more generalist. We quantified the degree of habitat specialization for a species, SSI, as the coefficient of variation (SD/mean) of its densities across habitats (using the 18 habitat classes recorded by observers during point counts) following Julliard et al.'s approach (2006).

Interestingly, this way of quantifying species' specialization can also be used with presence–absence data (Julliard et al. 2006). Indeed, assuming equal densities in occupied habitat and null density in others, a given species present in h habitat classes among H possible habitat classes would have a SSI equal to the square root of $(1/p - 1)$, were p is the proportion of occupied habitat classes (p = h/H). The log-transformed SSI will, in this case, be equal to $1/2 \ln (p/(1-p))$, i.e. $\ln(SSI) = -1/2 \text{logit}(p)$. Hence, if SSI is based on presence absence, the distribution of $\ln(SSI)$ is interestingly centered on zero, and symmetric (so that SSI gives opposite values for species present in i and H-i habitats). As counts of individuals (and not only their presence–absence) were available in the French breeding bird survey, we calculated SSI using counts of individuals to get the finest specialization measure. Then, for statistical analysis, these SSI values based on counts were further log-transformed to get more gradual specialization variation among species. We calculated a SSI for the 105 most

abundant terrestrial species, altogether representing more than 99% of the individuals detected by the FBBS.

As SSI is based on the calculation of the variance of densities in habitat classes, it is expected to be biased by low sample sizes. Indeed, errors of density estimation increases with decreasing sample sizes leading to a spurious increase in SSI values for low sample sizes. Given our large dataset, this bias was already shown to be very small by simulation study (Julliard et al. 2006). This bias can also be calculated explicitly. If one considers a perfect generalist species with a constant density in K habitat classes available in equal proportion, and if N is the total number of counted individuals, each class contains N/K individuals (so that SSI = 0). The mean estimated density is thus also N/K. Assuming that counted individuals in each class follow a Poisson distribution, the expected SSI (i.e. 0 + bias due to low sample size) is equal to the square root of N/K, divided by N/K (as the variance and the mean of a Poisson distribution are equals) which is equal to the square root of K/N. That is, all things being equal, the SSI bias decreases with increasing sampling effort.

We calculated the latter bias for each species given our data. It ranged from 0.03 to 0.57 whereas the raw SSI values were far more variable (from 0.224 to 2.238) and highly correlated to the corrected SSI values (raw SSI values minus expected SSI bias, $r^2 = 0.94$, n = 105). Therefore, only 6% of the SSI variation among species was induced by this intrinsic bias.

Note that SSI is not sensitive to the unequal representation of habitats in the sampling frame. Indeed, for a given specialist species, more individuals will be counted in habitats preferred by the species if these habitats are frequent (i.e. monitored by numerous point counts) than infrequent (i.e. monitored by few point counts). However, in both cases the density in these habitats (number of individuals counted in habitat classes divided by the number of point counts in habitats classes) will be similar. However, to compute a relevant SSI, one must define each habitat class with comparable ecological grain. For example, if one calculates the SSI using one class of forest and many farmland classes, forest birds will inevitably show higher SSI values than other species. Using a standardized and hierarchical land-use description is therefore useful to define comparable habitat classes. Finally, SSI is robust to the number of habitat classes considered. Indeed, even if among species SSI is less variable, one can still rank species from the less to the most specialized using SSI computed with fewer habitat classes (Julliard et al. 2004).

Landscape variables

Variables related to landscape fragmentation within each breeding bird survey plot were obtained from the CORINE Land Cover database by using the geographical information system package ArcView 3.2 (ESRI 2000). The former is a national geo-referenced land-cover, based on satellite digital images for the entirety of France. This land-cover was created in 1992 in order to classify, by means of remote sensing, habitat patches larger than 25 ha as belonging to one of 44 classes of habitat land use category (Bossard et al.

2000). The difference between two different habitat patches as well as the complex form of each patch is precisely given by CORINE. Each FBBS square was overlaid on this independent land cover database. Thus, each 2 × 2 km FBBS square encapsulated various number of habitat patches. We first sought to test whether specialist species were more negatively affected than generalists by habitat changes in space within a given landscape. For each FBBS square, we calculated the total contact length of the habitat patches provided by CORINE within the 2 × 2 km landscape (in km) as a measure of landscape fragmentation (the perimeter of the FBBS square measuring 8 km was systematically subtracted from this sum). This measure was highly correlated to the number of units and to the mean unit size in the landscape (respectively, r = 0.65, r = 0.78, n = 891). This metric is commonly used as a proxy for measuring landscape fragmentation (Lausch and Herzog 2002). Yet, this measure is not able to disentangle the habitat loss from the breaking apart within the landscape (Fahrig 2003). In this study, landscape fragmentation thus encompasses both habitat loss and habitat discontinuity within the landscape (Lindenmayer and Fisher 2006).

We also sought to test whether specialists were more negatively affected than generalists as habitat changes rapidly in time within a given landscape. This measure, thereafter called landscape disturbance, was provided by TERUTI, an independent landscape survey based upon a systematic grid made of 15 500 2 × 2 km squares. The TERUTI survey was specifically developed to estimate the variation in land-use throughout space and time for France (Agreste 2003). In each TERUTI square, 36 fixed sample points were monitored annually and assigned to one of a standard physical classification defined by 81 habitat categories. In each TERUTI square, the rate of change among the 81 habitat categories was calculated between 1992 and 2002 as a measure of landscape disturbance. Therefore, each TERUTI square had one disturbance value, which was null in the case of perfect landscape stability but which increased proportionally with habitat turnover rate.

We hypothesize that landscape disturbance and fragmentation should reduce the quality of habitats within the landscape for most species but particularly for specialist species. Therefore, fragmentation and disturbance were considered as two sources of habitat degradation for specialist species (Lindenmayer and Fisher 2006). Since the TERUTI and FBBS plots were designed independently, they were not always aligned. Therefore, kriging 200 interpolation was used to adapt disturbance measures to the FBBS plots distribution. This interpolation technique provided the best linear unbiased estimator of disturbance on FBBS plots with a spherical spatial model and using 20 neighbours (Cressie 1993, Ashraf et al. 1997).

Note that FBBS habitat data, which was used to calculate the specialization level of each species (SSI), CORINE and TERUTI surveys (respectively used to calculate landscape fragmentation and disturbance), were all collected on the same spatial scale of 4 km², but came from three different databases which were independent from each other.

Data analysis

We first sought to estimate, for each species, a response in terms of abundance distribution, to landscape fragmentation and disturbance. As fragmentation and disturbance were likely to be non-randomly distributed in space, we had to account for the inherent spatial gradient of these variables (Koening 1999, Carroll and Pearson 2000). This spatial autocorrelation issue is generally handled by spatial mixed model accounting for the autocorrelation structure. This type of model cannot handle count data (i.e. Poisson regression) for very large datasets. However, using coordinates (x, y) allows to control statistical analysis by differences in predictor variables induced by potential trend surface (Heikkinen and Birks 1996, Fortin and Dale 2005). We therefore used each term of a second order polynomial spatial regression based on coordinates as continuous variables ($S = x + y + x \times y + x^2 + y^2$).

We also constrained the statistical analysis of each species response to only habitat mostly preferred by the species. Indeed, the variation in abundance of any given species is ecologically meaningless in habitats where the species is never or only occasionally detected (e.g. a farmland species in forest habitats). We therefore selected, for each species, the subset of habitat classes among the 18, in which the density of the species was higher than the mean of the species density calculated across the 18 habitat classes. For a given species, the relationship between abundance and disturbance and fragmentation were thus estimated only in this subset of habitats (i.e. in the species preferred habitats). For a given species, there could still be systematic differences in abundance among its preferred habitat classes. We thus added habitat class (Hi) as a factor to the model (the levels of Hi correspond to the preferred habitat classes of species i). Thus, this first model was completed using the following equation separately for each species:

species' abundance$_i$

$$\sim S + H_i + \text{disturbance} + \text{fragmentation} \qquad (1)$$

For a given species, this first statistical model (Eq. 1) describes the variation of the species abundance in space, along gradients of disturbance and fragmentation, accounting for variation in abundance among its preferred habitats (H$_i$) and along a spatial trend surface (S). We considered the regression coefficients of disturbance and fragmentation effects on species' abundance provided by this model (Eq. 1) as the species-specific responses. Note that as the effects of fragmentation and disturbance were estimated simultaneously in the same model, each effect was adjusted to take account of the other so that each effect was not under-estimated (Starzomski and Srivastava 2007). This first analysis was conducted using the 8910 point counts (i.e. 891 FBBS sites of 10 point counts).

To test whether species-specific responses to fragmentation were related to specialization, we further performed a second GLM, with species-specific responses to fragmentation (i.e. using the 105 regression coefficients of the fragmentation effect given by Eq. 1) as dependent variable and specialization as an explanatory continuous variable (using the SSI values of the 105 species):

species response to fragmentation $\sim$ SSI $\qquad (2)$

One of the assumptions underlying Eq. 2 is that each species response to fragmentation provides equally precise information about the deterministic part of the total process variation. In other words, the standard deviation of the error term is assumed to be constant over all values of the predictor or explanatory variables. This assumption, however, clearly does not hold here because depending on the sample size, the precision of the response to fragmentation (or disturbance) provided by Eq. 1 could vary substantially from one species to another. Equation 2 was thus modelled using a weighed GLM in which precision associated with each estimate was incorporated as a weight into the fitting criterion (using the inverse of the squared standard error of the regression coefficient of the fragmentation effect provided by Eq. 1). Using these weights in optimizing the weighted fitting criterion to find the parameter estimates accounts for the error contribution of each observation to the final parameter estimates (Carroll and Ruppert 1988, Ryan 1997). The same model was performed separately with species-specific responses to disturbance.

To seek out hidden non-linear relationships in Eq. 2, we plotted results of the corresponding General additive model (GAM), which were analogous to the weighted GLM, but able to handle non-linear data structures and non-monotonic relationships between the response and the predictive variable (Siriwardena et al. 1998, Guisan et al. 2002). Hence, in these plots, specialization was considered as a smooth term using 3 DF. All analyses were conducted using nlme and mgcv packages of the R statistical software ver. 1.9.1.

Finally, we sought for spurious links between fragmentation (or disturbance) and SSI calculation (i.e. relationships not based on ecological processes). Indeed, if, for any reason, species tended to have higher SSI values in fragmented landscapes, our results linking SSI and fragmentation could be circular. We therefore sought for a direct measure of SSI robustness to fragmentation and disturbance. We thus independently calculated SSI in more or less fragmented landscapes to quantify the effect of fragmentation on SSI itself (the same was done for disturbance). To test SSI robustness to fragmentation (and disturbance), we first ordered all FBBS plots according to their level of fragmentation (or disturbance). As SSI is sensitive to the number of individual counted (but not influenced by the number of plot surveyed), we divided, for each species, the raw dataset in five centiles, each including equal numbers of individuals. Hence, for a given species, SSI calculated in each centile can be safely compared.

We repeated the SSI computation for each species in each centile in order to get, for each species, five SSI values, each calculated in a subset of sites with a given fragmentation (or disturbance) level (from one to five).

Finally, to quantify the potential systematic difference between SSI values calculated in more or less fragmented plots, we further tested whether and how the average SSI of each species, calculated using plots of the two less fragmented centiles, were related to the average SSI values calculated using plots of the two most fragmented centiles (using pairwise t-test on the 105 species). The same analysis was done with disturbance.

Results

We found that species response to landscape fragmentation was strongly negatively related to the Species specialization index (GLM: $F_{1, 103} = 38.38$, $p < 0.0001$, $r^2 = 0.27$, Fig. 2A). We also found that species response to landscape disturbance was strongly negatively related to the Species specialization index ($F_{1, 103} = 9.51$, $p < 0.001$, $r^2 = 0.09$, Fig. 2B). A close inspection of each species response allowed us to refine previous general findings. We found that among the 105 species, respectively 61 and 44 species showed negative and positive responses to spatial fragmentation (Supplementary material). Similarly, respectively 56 and 49 species showed negative and positive responses to temporal disturbance.

Moreover, the links between specialization and response to landscape fragmentation (Fig. 2A) or temporal disturbance (Fig. 2B) were not linear (the p-values for the two smoothed terms using GAM with 3 DF were both less than 0.0001 for fragmentation and disturbance). Instead of a linear trend, theses curves suggested that the more specialist a species was, the strongest it was affected by fragmentation

and disturbance. In other words, specialists were affected more negatively than generalists.

Concerning the potential spurious link between SSI and fragmentation, we found that SSI values tended to be lower in more fragmented landscapes, but this systematic difference was very low regarding the among species variation of SSI (SSI calculated in less fragmented plots minus mean SSI calculated in most fragmented plots: 0.17, paired t-test on 105 DF, $p < 0.001$). Moreover, SSI values calculated in the most and in the less fragmented landscapes were highly correlated ($r^2 = 0.81$, $n = 105$, $p < 0.001$, Fig. 3A). We found no difference between SSI values in the most and less disturbed plots (mean difference: 0.094, paired t-test on 105 DF, $p = 0.12$). Finally, SSI calculated respectively in the two most and the two less disturbed centiles were highly correlated ($r^2 = 0.77$, $n = 105$, $p < 0.001$, Fig. 3B).

Discussion

We showed that specialist species tended to be located in less fragmented and less disturbed landscapes than generalists. These results were found in relating for a given species, a measure of the strength of its habitat specialization (i.e. the species specialization index, SSI), and its spatial distribution along gradients of landscape disturbance and fragmentation, measured independently by two different land-cover databases. Spatial variation in abundance of a given species is generally believed to reflect the extent to which local sites satisfy the species' niche requirements (Brown et al. 1995). Here, we showed a systematic difference between the spatial distribution of "winners" and "losers" along large scale gradients of habitat fragmentation and disturbance.

We expected most species to be negatively affected by fragmentation and disturbance and specialists to be even more negatively affected than generalists. In fact, our results show that sources of landscape degradation divided species in two equal sized groups: half of the species were negatively affected while the other half benefited from landscape fragmentation and/or disturbance. Therefore, in a given community, there might be as many losers as winners. This can result in species assemblages with unchanged species richness, but considerable change in species composition. This pattern might reflect the functional homogenization process in which some species systematically replace other more specialist species (Devictor et al. 2007b).

Such relationships could be circular if species more abundant in unfragmented landscape appeared to be specialized and if, conversely, species more abundant in fragmented landscapes appeared to be generalist. We checked this by calculating the species specialization index (SSI) in two subsets of the data including respectively the most and the less fragmented landscapes (the same analysis was done for disturbance). We showed that SSI values were underestimated in more fragmented landscapes. In fact, it is likely that in highly fragmented landscapes, a point count monitored in a given habitat type (e.g. in farmland) was more often surrounded by other habitat types (e.g. forest fragments). Consequently, species occurring in different habitat types were closer from each other in more fragmented landscapes. It is thus likely that in fragmented
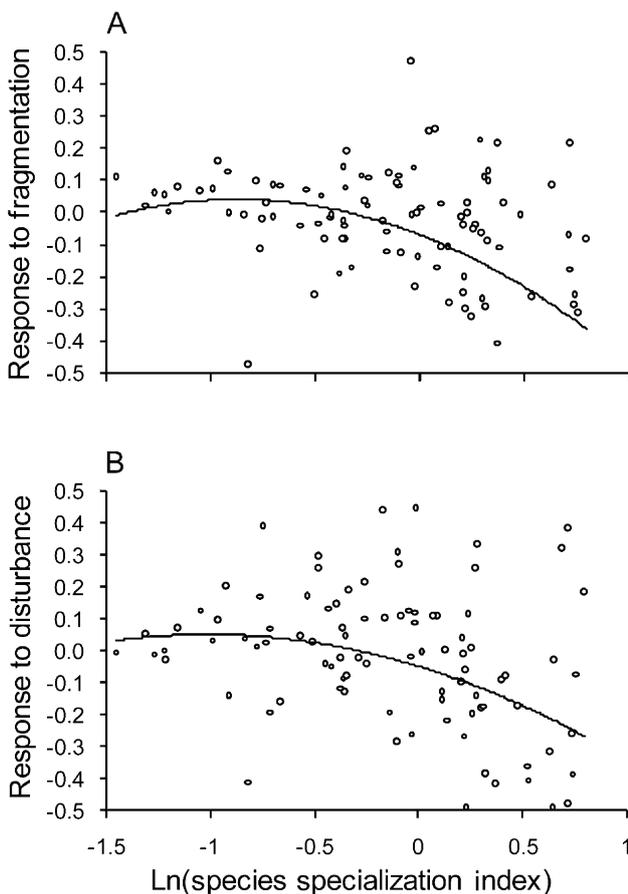

Fig. 2. (A) Spatial distribution of more or less specialized species, along a habitat fragmentation gradient, (B) Spatial distribution of more or less specialized species, along a habitat disturbance gradient. Each species distribution was previously estimated by a GLM model controlling for a second order polynomial spatial trend and its preferred habitat classes (among all monitored point counts, $n = 8910$). Smoothed plots were obtained using GAM models with 3 DF.
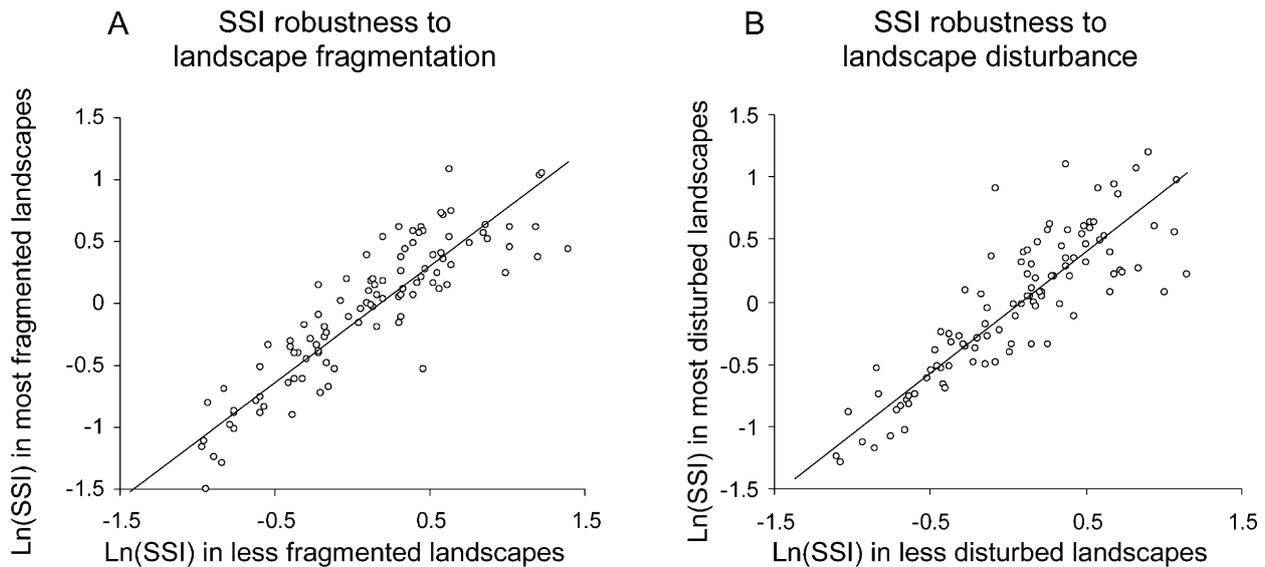
Fig. 3. SSI robustness to (A) landscape fragmentation and (B) disturbance. Relationship between SSI calculated in the most and in the less fragmented landscapes. SSI was calculated independently for each species in five centiles of increasing fragmentation (or disturbance), comprising the same number of individuals. The plot represents the relationship between the average SSI of the two less and the most fragmented (or disturbed) centiles for each species.

landscapes, observers have recorded species as occurring in a given habitat type although the species was located in another surrounding one (e.g. in fragmented farmland, observer often see and hear species in surrounding forest fragments). In this case, individuals were associated with higher number of habitat classes so that SSI was biased towards low values.

However, we showed that this underestimation was very low (i.e. the systematic differences of SSI values due to fragmentation, and disturbance, were very low compared to the among species variation of SSI) and not biased: a specialist and a generalist species had respectively high and low SSI either in fragmented (or disturbed) and unfragmented (or undisturbed) landscapes. Therefore, even if SSI is not flawless, it is unlikely that our results are driven by the way SSI was calculated.

Our results are consistent with the prediction that, as generalists use various habitat types in the landscape matrix, they should be less affected by habitat fragmentation than specialists, which are more dependent on one or few habitat types (Brouat et al. 2004). Specialists are also expected to be negatively affected by landscape disturbance as natural selection has favored their development in stable environments (Futuyma and Moreno 1988, Kithahara et al. 2000, Kassen 2002). These results are also consistent with empirical findings suggesting that the decline of specialist species observed worldwide is likely to be related to human-induced landscape degradation (Steffan-Dewenter and Tscharntke 2000, Kotze and O'Hara 2003, Krauss et al. 2003, Devictor et al. 2007a, 2007b).

Although we found that specialist species tended to be located in less fragmented and less disturbed landscapes than generalists, we also found a very high variation around these tendencies. This high variability in species responses mainly reflects that there are many drivers of the spatial distribution of species abundance which differ from fragmentation and disturbance. Moreover, many fragmen-

ted landscapes probably enclose old and stable fragments, allowing, in some cases, specialists to colonize and prosper in these fragments. We thus anticipate some situations where highly specialized species can survive in disturbed habitats (Attum et al. 2006).

We also showed that, on average, the number of counted individuals tended to decrease faster with increasing landscape fragmentation and disturbance for more specialized species than for generalists. This asymmetry between specialists and generalists' abundance distribution along fragmentation and disturbance gradients may be induced by the difference in ecological mechanisms involved in specialist or generalist responses. Indeed, specialists are likely to be affected directly by landscape degradation while generalists are more probably positively influenced by competitive relaxation with specialists than by direct modifications of the landscape (Marvier et al. 2004).

Each species vulnerability to different risks is determined by the species' own ecology (Owens and Bennett 2000). For example, diet, migratory strategy, or body mass were also previously shown to be good predictors of species vulnerability to human disturbance (Blumstein et al. 2005). But the fact that habitat specialist species should be more affected by landscape disturbance and fragmentation should be consistent despite variation in other functional traits (McKinney 1997). Therefore, SSI cannot tell which of these parameters is likely to affect a given species response, but rather integrates any of these life history traits in a single parameter which is comprehensive and robust. We suggest that this measure of specialization can be considered as a holistic functional trait which should be useful in community and ecosystem ecology (McGill et al. 2006, Violle et al. 2007).

Any multi-species analysis could be hindered by taxonomic relatedness among species. We used Moran's I metric to test if, within a taxonomic level, species were more similar regarding their specialization (SSI) than expected by

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chance. Moran's I metric quantifies the degree of clustering of a given trait at each taxonomic level (Order, family, genus) for a given list of species (Lockwood et al. 2002). We did not find such taxonomic autocorrelation in this trait at any taxonomic level ($I_{order} = 0.02$, $p = 0.35$; $I_{family} = -0.01$, $p = 0.8$; $I_{genus} = -0.09$, $p = 0.48$). In other words, our specialization measure was not clustered according to these three taxonomic levels.

Finally, our abundance estimates based on point-counts were not true abundances as not all individuals were detected during FBBS visits. In addition to imprecise abundance estimate, variation in detectability could have induced other hidden bias if, for instance, we had over-estimated the negative effect of fragmentation on specialized species because these species had a lower detection probability in more fragmented landscapes. That species are not equally detected was previously emphasized (Boulinier et al. 1998) as well as the fact that detectability can vary across habitats (Thompson 2002). However, our results could be weakened only if there was an interaction between species' specialization and spatial fragmentation on detectability. This interaction must also lead to the pattern we found when considering landscape disturbance.

Even if promising frameworks are now available to estimate species' abundance while accounting for sources of variation in detectability, the latter require either a co-variable linked to detection probability (e.g. a distance from observers and individuals; Buckland et al. 2006) or repeated visits to the same point counts in time (Royle et al. 2005). So far, data coming from the FBBS scheme cannot be handled by such techniques. However, we see neither methodological reasons nor ecological meaning for the interaction between specialization, fragmentation (or disturbance) and detectability.

The dual forces of habitat modification and climate change are expected to cause more specialist species to decline, leaving biological communities with reduced numbers of species, and dominated by mobile and wide-spread habitat generalists (McKinney and Lockwood 1999, Warren et al. 2001). This symptom of biodiversity loss has received recent attention because the identity, abundance and range of species traits, appear to be what matters most in ecosystem services (Diaz et al. 2006). In this respect, we suggest that measuring the opposing responses of more or less specialized species to habitat fragmentation and disturbance is relevant to narrow-down conservation options and to develop new theoretical investigations to predict who wins the game in the current biodiversity crisis.

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Supplementary material. Appendix 1 can be found at www.oikos.ekol.lu.se/appendix as Appendix O16215