RESEARCH PAPER

Functional biotic homogenization of bird communities in disturbed landscapes

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ABSTRACT

Aim Worldwide, functional homogenization is now considered to be one of the most prominent forms of biotic impoverishment induced by current global changes. Yet this process has hardly been quantified on a large scale through simple indices, and the connection between landscape disturbance and functional homogenization has hardly been established. Here we test whether changes in land use and landscape fragmentation are associated with functional homogenization of bird communities at a national scale.

Location France.

Methods We estimated functional homogenization of a community as the average specialization of the species present in that community. We studied the spatial variation of this community specialization index (CSI) using 1028 replicates from the French Breeding Bird Survey along spatial gradients of landscape fragmentation and recent landscape disturbance, measured independently, and accounting for spatial autocorrelation.

Results The CSI was very sensitive to both measures of environmental degradation: on average, 23% of the difference in the CSI values between two sample sites was attributed to the difference in fragmentation and the disturbance between sites. This negative correlation between CSI and sources of landscape degradation was consistent over various habitats and biogeographical zones.

Main conclusions We demonstrate that the functional homogenization of bird communities is strongly positively correlated to landscape disturbance and fragmentation. We suggest that the CSI is particularly effective for measuring functional homogenization on both local and global scales for any sort of organism and with abundance or presence–absence data.

Keywords
Biodiversity indicator, bird, breeding bird survey, biotic homogenization, community, France, landscape fragmentation, landscape disturbance, specialization, 2010 target.

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INTRODUCTION

Emerging evidence suggests that biotic homogenization is a major response to global changes. Biotic homogenization has three components: genetic, taxonomic and functional (Olden *et al.*, 2004). Taxonomic homogenization (the most well known component) is the increase in species similarity in space over time, whereas functional homogenization of communities is measured as a decrease in functional diversity among species in the community (Olden & Rooney, 2006). Ecological mechanisms leading to the functional homogenization of a given species assemblage represent specific and quite different processes from those involved in taxonomic homogenization (Olden, 2006). In particular, functional homogenization is dependent on the trait of interest and need not to be linked to either species invasion or extinction.

In this respect, many studies have recently emphasized that specialist species are more likely to be negatively affected by current global changes than generalists (McKinney & Lockwood, 1999; Warren *et al.*, 2001; Julliard *et al.*, 2004; Rooney *et al.*, 2004).

This pattern is now considered as a major trend in biodiversity loss which should lead to the functional homogenization of communities (McKinney & Lockwood, 1999; Olden *et al.*, 2004). Yet driving forces of functional homogenization in natural communities as a result of current global changes have hardly been investigated at a large scale (but see Devictor *et al.*, 2007).

One difficulty in quantifying the responses of biodiversity to large-scale human pressures is that biodiversity is multifaceted (Purvis and Hector, 2000). Therefore, most studies have evaluated the causes of community changes in space and time in two steps. First, patterns of species assemblage in space and/or time were documented through integrative measures such as species richness or diversity. Second, the most likely explanations were extrapolated to explain the observed pattern This approach is common in macroecological studies in which experimental designs are generally not possible (Blackburn & Gaston, 2003).

When studying the causes of functional biotic homogenization, these two steps can be usefully inverted. Indeed, strong theoretical responses of specialist versus generalist species to disturbance are expected a priori. Theory predicts that environmental constancy (in space and/or time) should favour specialists, whereas generalists should benefit from the lack of stability of the environment (Levins, 1968; Futuyma & Moreno, 1988; Kassen, 2002; Marvier *et al.*, 2004). Consequently, environmental degradation induced by global changes should not only affect specialist species negatively, but may well benefit generalists (McKinney & Lockwood, 1999).

Measuring functional homogenization through integrative continuous measures should therefore be very useful for both applied and theoretical investigations. Indeed, we sorely miss indices reflecting if, and how, human-induced disturbances and biodiversity interact at a large scale (Balmford *et al.*, 2005a,b). The fact that functional homogenization is expected to be strongly linked to environmental degradation should confer interesting predictive properties upon such a measure.

When measuring functional homogenization, species are generally only considered as either specialist or not for a given resource, despite an obvious continuum of specialization level across species for several resources (Berenbaum, 1996; Fridley *et al.*, 2007). Recently, Julliard *et al.* (2006) have quantified specialization of species as the coefficient of variation (standard deviation/average) of their densities among habitat classes. Such a species specialization index (SSI) should be useful to build a sensitive (yet simple) index of biotic homogenization at the community level. This community index could, in turn, be used to test the role played by human-induced disturbance in functional biotic homogenization.

Moreover, measurement of the process of functional homogenization should overcome an often inherent compromise in the development of biodiversity indicators: the choice between an indicator which is easily interpretable in any habitat (and at any spatial scale) and an indicator which is applicable to the maximum number of species. It should have the great advantage of tackling the fate of both specialists and generalists simultaneously while, at the same time, still being meaningful.

In this paper we measured the community specialization index (CSI) of birds, which estimates functional homogenization as the average specialization of the individuals (SSI) of species present at a given site. We investigated the response of the CSI to the two principal driving forces of anthropic biodiversity loss in terrestrial ecosystems: habitat fragmentation and disturbance (Vitousek *et al.*, 1997). Two independent land-cover surveys were used to quantify these pressures. The sensitivity of the CSI was further tested across habitats and biogeographical zones to confirm the robustness of the relationships.

METHODS

Bird data

We used data from the French Breeding Bird Survey (BBS), a standardized monitoring programme in which skilled volunteer ornithologists identify breeding birds by song or visual contact each spring (Julliard & 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 farmlands, woodlands, suburbs and cities) (Fig. 1). Each plot ($n = 1028$) was monitored by two annual visits in spring, one before and one after 8 May, with 4−6 weeks between the two visits. To be validated, the count had to be repeated on 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). In each plot, the observer carried out 10 evenly distributed point counts, within which each individual from species heard or seen during a 5-min period was recorded. Point counts were 300 m apart and sampled in the
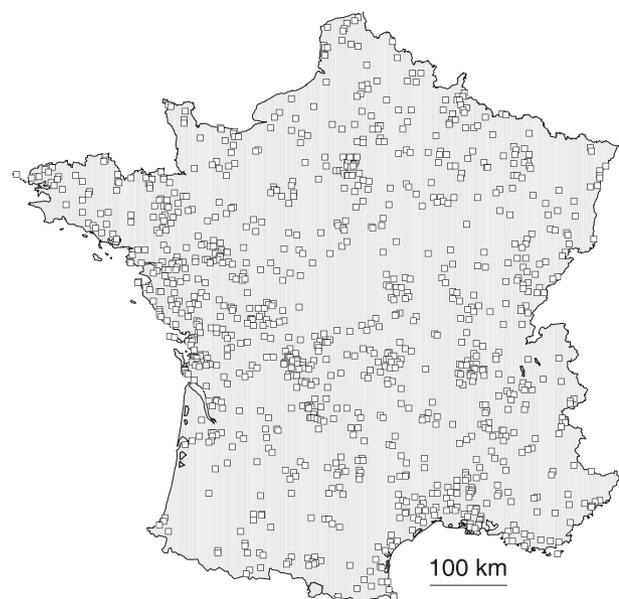

Figure 1 Spatial distribution of Breeding Bird Survey plots. Each plot is a 2×2 km square in which 10 point counts are evenly distributed. Each point was monitored between 2001 and 2004 and used to compute a community specialization index (CSI).

same order. For a given point count, the maximum counts of the two annual visits were retained and then averaged over 4 years (2001–04).

For each point count, the surroundings within a fixed 100-m radius were classified by observers as belonging to one of a standardized list of habitats. This list was organized into a standardized four-level land use description, adapted from the one developed by the British Trust for Ornithology (Crick, 1992). In this paper, we use the first two levels of this habitat description. The first level is a coarse division into four main habitat categories: farmland, natural, artificial and a final 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. Each habitat class was covered by at least 100 point counts.

Measuring functional homogenization

The degree of specialization of a species for a given resource may be described by the pattern of the species' abundance along that resource gradient (Austin *et al.*, 1990). Intuitively, a given species is more specialized to some habitat classes if its density there is higher than elsewhere. Conversely, a species whose density varies little across habitats can be considered a more generalist species.

We used the approach of Julliard *et al.* (2006) to quantify each SSI and the average specialization index of the community. These authors used the coefficient of variation (standard deviation/ mean) of the species density across habitats as a measure of habitat specialization (SSI). Then, a CSI was calculated as the average specific specialization index of all individuals detected in a given plot (Julliard *et al.*, 2006).

As their SSI was based on variance calculations of densities in habitat classes, it was expected to be biased by low sample sizes. Indeed, as errors of density estimation inevitably increased with decreasing sample size, SSI was also spuriously higher for low sample sizes. However, for our large data set, our bias will be very small given their findings (Julliard *et al.*, 2006). This bias can also be calculated explicitly. If we consider a perfect generalist species as having a constant density in K habitat classes (with each habitat available in equal proportion), and n is the total number of counted individuals, each class is expected to contain the same n/K individuals, so that, in theory, SSI = 0. 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 K/n. That is, all other things being equal, the SSI bias decreases with increasing sampling effort. We calculated such bias for each species given our data. It ranged from 0.03 to 0.45. 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, $r^2 = 0.96$, $n = 100$). Therefore, only 4% of variation in SSI among species was induced by this intrinsic bias.

Using SSI, all considered species are ranked from the most to the least habitat dependent, whatever their size, ecology and habitat preference and under any habitat classification. Moreover, SSI can be calculated with presence–absence data (Julliard *et al.*,

2006). To compute this SSI, we utilized the $K = 18$ habitat classes recorded by observers during point counts. 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. The SSI was calculated for the 100 most frequently detected terrestrial bird species in the 10,280 point counts. These birds represented 99% of the censused individuals (excluding water birds). All species considered were detected at least 200 times.

The CSI was then calculated for each 2×2 km BBS plot as the average specific specialization index of all individuals detected. The CSI in plot j is thus given by

$$\mathrm{CSI}_j = \frac{\sum_{i=1}^{n} a_{ij}(\mathrm{SSI}_i)}{\sum_{i=1}^{n} a_{ij}}$$

where n is the total number of species recorded, a_{ij} is the abundance of individuals of species i in plot j, and SSI_i its specialization index.

Landscape variables

Fragmentation measure

We predicted that specialist species are more negatively affected than generalists as habitat changes rapidly in space within a given landscape. We therefore sought to measure spatial instability of habitats within landscape plots. The loss of habitat and the breaking apart of habitat are generally confounded when measuring fragmentation (Fahrig, 2003). Here, we were not able to disentangle both aspects of the fragmentation process (habitat loss and true fragmentation). We thus used the sum of all contact lengths of polygons within landscape elements (in kilometres) as a surrogate to measure habitat instability of the landscape (the perimeter of the plot measuring 8 km was systematically subtracted from this sum). The latter was provided by the CORINE Land Cover data base and by using the geographical information system package ArcView 3.2 (ESRI, 2000).

CORINE is a national georeferenced land-cover data base, based on satellite digital images for the whole of France. This land-cover layer was created in 1992 in order to classify, by means of remote sensing, landscape units larger than 25 ha as belonging to one of 44 classes (Bossard *et al.*, 2000). Although a polygonal area needed to be greater than 25 ha to be reported on CORINE, the resolution concerning polygon limits is 20 m. In other words, the difference between two polygons of different habitat type as well as the complex form of each polygon was precisely represented by CORINE. The sum of all contact length polygons was thus considered as a good measure of habitat discontinuity. The latter was highly correlated with the number of polygons and with the average polygon size of the different habitat types enclosed in the landscape. This metric is also commonly used as a proxy for measuring landscape fragmentation (Lausch & Herzog, 2002). We therefore expected that, as specialists should be more negatively affected by habitat discontinuity in the landscape, low CSI values should be associated with high total contact length of polygons.

Disturbance measure

Habitat disturbance affecting landscapes between 1992 and 2002 was provided by TERUTI, an independent national 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 the whole of 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. Each TERUTI square had one disturbance value, which was null in the case of perfect landscape stability. Conversely, this measure increased in proportion to habitat turnover rates. Since the TERUTI and BBS plots were designed independently they were not always aligned. Therefore, a kriging interpolation technique was used to adapt disturbance measures to the BBS plot distribution. This interpolation technique provided the best linear unbiased estimator of disturbance on BBS plots (Cressie, 1993; Ashraf *et al.*, 1997).

Note that BBS habitat data, which served to calculate the level of specialization of each species (SSI), and the CORINE and TERUTI surveys, which served to calculate landscape fragmentation and disturbance, respectively, were all collected on the same spatial scale of 4 km^2, but were entirely independent of each other.

Statistical analysis

We tested the relationships between CSI and landscape variables in three steps. In all the following models, the effects of fragmentation and disturbance were tested simultaneously in the same models. Thus each effect was adjusted to take account of the other.

First, as CSI values were likely to vary across the different habitats in which point counts were conducted, we used a generalized linear model (GLM) with CSI as the dependent variable and BBS habitat as a factor (i.e. using the habitat documented in the field by observers in each point count, among the 18 habitat classifications). This first analysis, called step 1, was conducted using the 10,280 point counts (i.e. 1028 BBS plots of 10 point counts). We then used the estimates provided by this first analysis to obtain habitat-adjusted CSI values for each BBS plot.

In the second step, as CSI, fragmentation and disturbance were likely to be non-randomly distributed in space, we had to account for potential spatial autocorrelation between samples (Carroll & Pearson, 2000; Legendre *et al.*, 2002; Rangel *et al.*, 2006). To do so, we ran GLM models that assumed no spatial structure between errors with habitat-adjusted CSI (calculated in step 1) as the dependent variable, and disturbance and fragmentation as the explanatory continuous variables. We then used semivariograms of this prior analysis as a tool for investigating spatial autocorrelation structure (Fortin, 2002). We then ran a general linear mixed model (GLMM) allowing for spatial dependence in the errors by defining the spatial correlation

structure (range and nugget) inherited from the semivariogram analysis (Lin & Zhang, 1999). To seek out hidden nonlinear relationships, we then plotted the results of the corresponding general additive mixed model (GAMM), which were analogous to the GLMM but able to handle nonlinear data structures and non-monotonic relationships between the response and predictive variables (Siriwardena *et al.*, 1998; Guisan *et al.*, 2002). Hence, in this latter model, fragmentation and disturbance were considered as smoothed terms and the model plots reflected each effect, adjusted for the other one, accounting for spatial dependence. We reported numerical results of GLMM and plots of GAMM.

A third step was performed to confirm that our results were robust across habitats and biogeographical zones. Robustness across habitats was tested by omitting step 1 (standardization by habitat) and by running the models (step 2) using the subset of point counts monitored in natural (i.e. woodlands, scrublands and grasslands; $n = 3210$), farmland ($n = 5087$) or artificial ($n = 1544$) habitats separately. The other 439 point counts out of 10,280 were classified as other habitat types and thus excluded from this analysis. These subsets were obtained using the first level of the BBS habitat classification recorded by observers in the field. Similarly, we wanted to confirm that our results were robust across biogeographical zones. We thus used habitat-adjusted CSI values (calculated in step 1) to perform all previous models (step 2) separately for the three subsets of BBS plots monitored in the three biogeographical zones encompassed by France (Atlantic $n = 517$; Mediterranean $n = 151$; Continental $n = 360$). All analyses were conducted using nlme and mgcv packages of R statistical software version 1.9.1 (R Development Core Team, 2004).

RESULTS

Among the 100 common species considered in this study, the SSI ranged from 0.228 for the most generalist species (*Turdus merula*) to 2.227 for the most specialized species (*Vanellus vanellus*). At the community level, when considering all monitored plots together, a strong negative relationship between CSI and both spatial fragmentation and temporal disturbance was detected (adjusted fragmentation and disturbance effects, GLMM on 1028 d.f.: respectively, $t = -9.0$, $P < 0.0001$, Fig. 2a; $t = -3.8$, $P < 0.001$, Fig. 2b; $R^2 = 23\%$).

The same pattern was detected when grouping BBS plots according to each major habitat type. Indeed, when the analysis was performed only on point counts defined as farmland by observers, we found strong negative correlations between CSI and both fragmentation and landscape disturbance (GLMM on 909 d.f.: respectively, $t = -9.73$, $P < 0.0001$; $t = -5.32$, $P < 0.0001$; $R^2 = 28\%$, Fig. 3a). Similarly, CSI calculated on point counts located in habitat noted as natural, or artificial, were also strongly negatively correlated with landscape fragmentation as well as with landscape disturbance (natural habitats, GLMM on 801 d.f.: respectively $t = -4.84$, $P < 0.0001$; $t = -2.68$, $P = 0.007$; $R^2 = 8\%$, Fig. 3b; and artificial habitat, GLMM on 675 d.f.: respectively, $t = -3.14$, $P = 0.0017$; $t = -2.78$, $P = 0.005$; $R^2 = 7\%$, Fig. 3c).
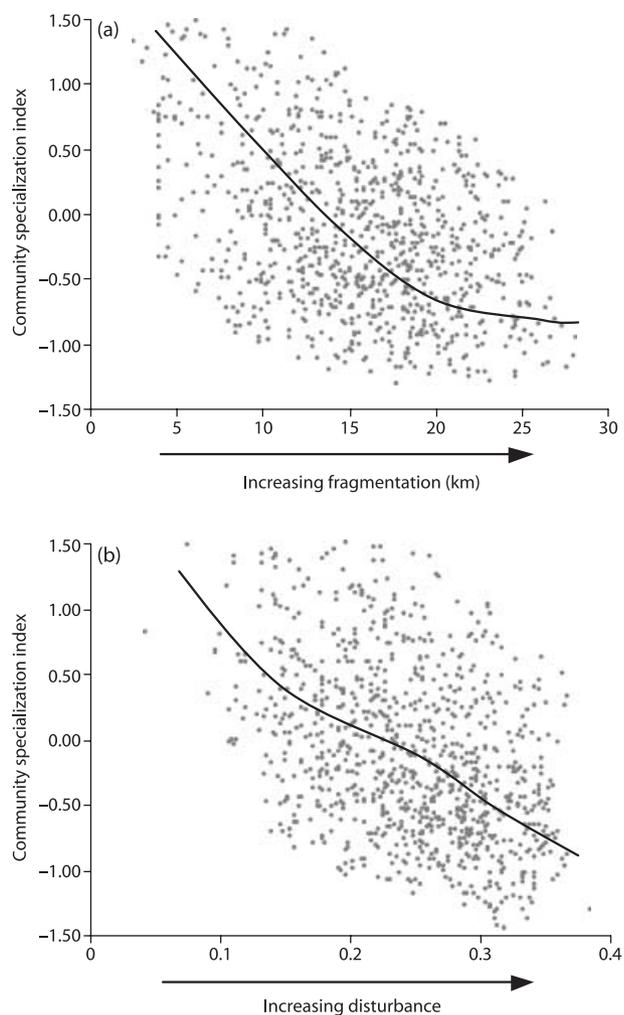
Figure 2 Relationships between the community specialization index (CSI) and landscape fragmentation or disturbance. The relationships between (a) CSI and fragmentation (in km) or (b) disturbance are tested accounting for habitat type (habitat was taken as a factor in the model), using all monitored point counts ($n = 10,280$). Smoothed curves are obtained with generalized additive mixed models (GAMM) taking spatial dependence between samples into account.

Finally, using habitat-adjusted CSI values for the Atlantic biogeographical zone point counts, we found once more that CSI was negatively correlated with landscape fragmentation and disturbance (GLMM on 517 d.f.: respectively, $t = -6.52$, $P < 0.0001$; $t = -3.13$, $P = 0.001$; $R^2 = 26\%$, Fig. 4a). The same pattern was detected in the Mediterranean (GLMM on 151 d.f.: respectively, $t = -3.48$, $P < 0.0001$; $t = -3.51$, $P < 0.001$; $R^2 = 16\%$, Fig. 4b) and Continental biogeographical zones (GLMM on 360 d.f.: respectively, $t = -5.76$, $P < 0.0001$; $t = -3.30$, $P = 0.001$; $R^2 = 35\%$, Fig. 4c).

DISCUSSION

We found strong negative relationships between the CSI and both landscape fragmentation and disturbance. These results

reflect ecologically important processes. Since 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 a few habitat types (Brouat *et al.*, 2004). Specialists are also expected to be negatively affected by landscape disturbance since natural selection has favoured their development in stable environments (Futuyma & Moreno, 1988; Kithahara *et al.*, 2000). On the contrary, generalists should benefit from competitive relaxation with specialists in disturbed landscapes. Most of these processes were theoretical and had no empirical support.

In macroecological studies, the vulnerability of species to global changes is often related to the geographical distribution of the species, its niche property and/or its thermal tolerance (Jiguet *et al.*, 2006). This species by species approach was shown to be relevant to the prediction of future species distribution (Broennimann *et al.*, 2006) or current dynamics (Julliard *et al.*, 2004; Jiguet *et al.*, 2007). At the community level, impacts of global changes have mainly been investigated through non-functional measures such as species richness (Higgins, 2007; Lemoine *et al.*, 2007). Further community attributes were studied by looking at how non-native species tend to homogenize communities (McKinney, 2004; McKinney & La Sorte, 2007) or at how human pressures could change the proportion of common and rare species (La Sorte, 2006). Here, we showed that measuring functional homogenization through the quantification of species specialization is an interesting complementary approach that provides highly predictive measures of the impact of human pressure on community composition.

Determining the fate of biodiversity through relevant indicators is a current scientific challenge of great importance (Balmford *et al.*, 2003, 2005a,b). A biodiversity indicator should ideally reflect changes in biodiversity, properly link these changes to specific pressures and be rooted in sound scientific theory (Gregory *et al.*, 2005). In practice, most biodiversity indicators are deprived of ecological meaning so that their trends are very difficult to interpret. In addition, their sensitivity to current global changes is actually hardly tested, and therefore it is not clear whether (and how) such indicators can be related to anthropogenic perturbations. One difficulty in finding an indicator which reflects human pressures is that biodiversity loss is scale dependent, such that a given biodiversity indicator, defined for a particular scale (e.g. that of a country), can be inappropriate at another scale.

But functional biotic homogenization is embodied by a consistent trend: the global decline of specialist species worldwide (losers) progressively replaced by more tolerant and generalist species (winners) (McKinney & Lockwood, 1999). We thus propose the use of CSI as a biodiversity indicator based upon the quantification of SSIs as a means of measuring community responses to habitat degradation. We believe that such an index is likely to greatly improve the current set of biodiversity indicators because it is a priori expected to reflect well-identified pressures, and therefore its trends will be directly interpretable. In addition, rather than focusing on a particular subset of species that are generally selected by expert judgement (e.g. farmland bird specialists), our results generalize existing indicators relying on
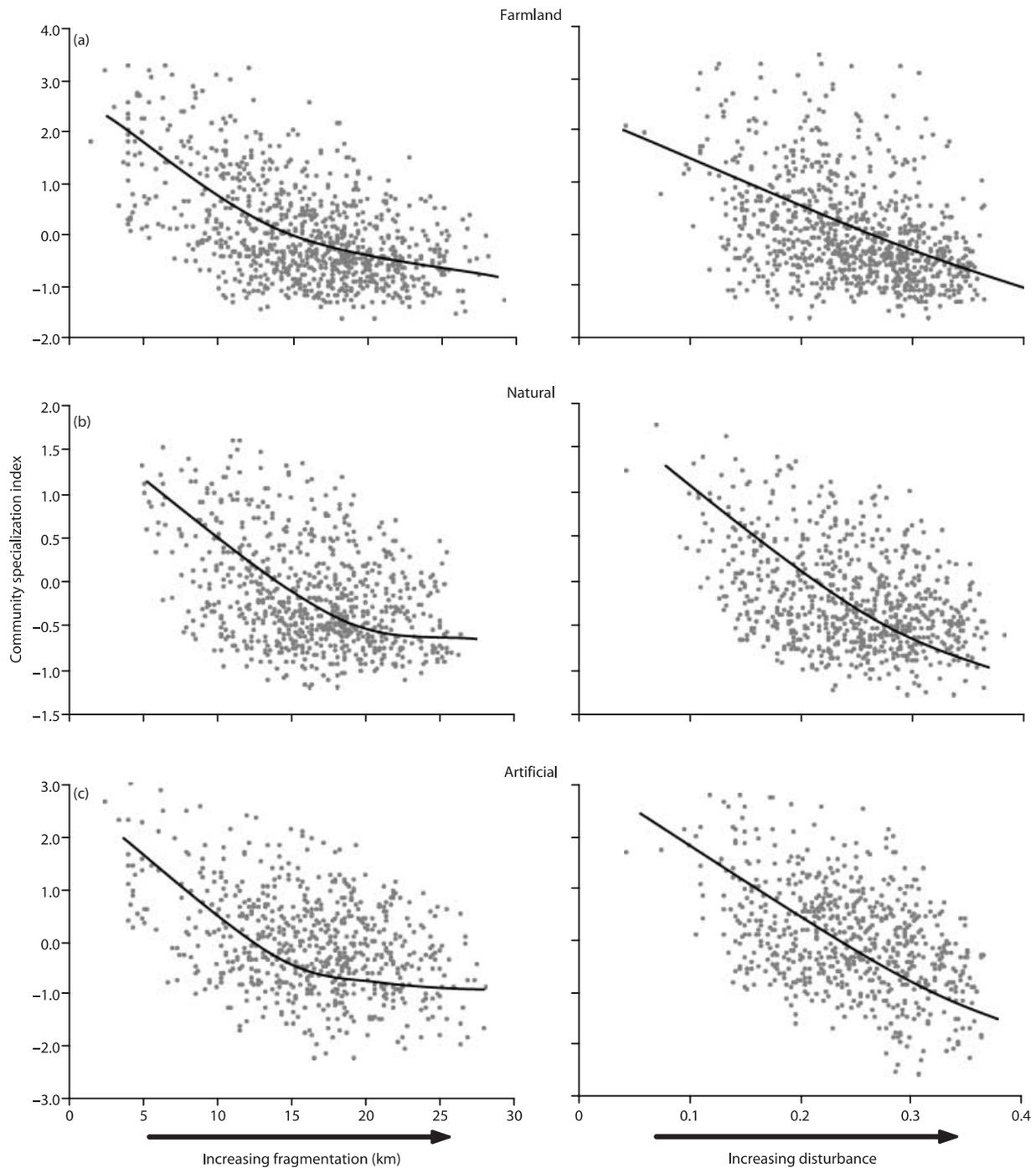
Figure 3 Relationships between the community specialization index (CSI) and landscape fragmentation or disturbance within each habitat type. The relationships between CSI and fragmentation (in km) or disturbance are tested using point counts monitored in (a) farmland ($n = 5087$), (b) natural ($n = 3210$) or (c) artificial habitats ($n = 1544$). Smoothed curves are obtained with generalized additive mixed models (GAMM) taking spatial dependence between samples into account.

subsets of species. In enclosing all species (and not only those negatively affected, or those of a fixed particular list), CSI should be more powerful and integrative than other metrics while being applicable across countries and scales.

Indeed, considering France as a whole, without distinctions for habitats or biogeographical zones, we first found a negative

relationship between CSI and both fragmentation and disturbance. The statistical power of these relationships was striking for such data: on average, 23% of the difference in CSI values observed between two points was predicted by fragmentation and recent disturbance of the landscape. Then we showed that the CSI response remained qualitatively unchanged within habitat
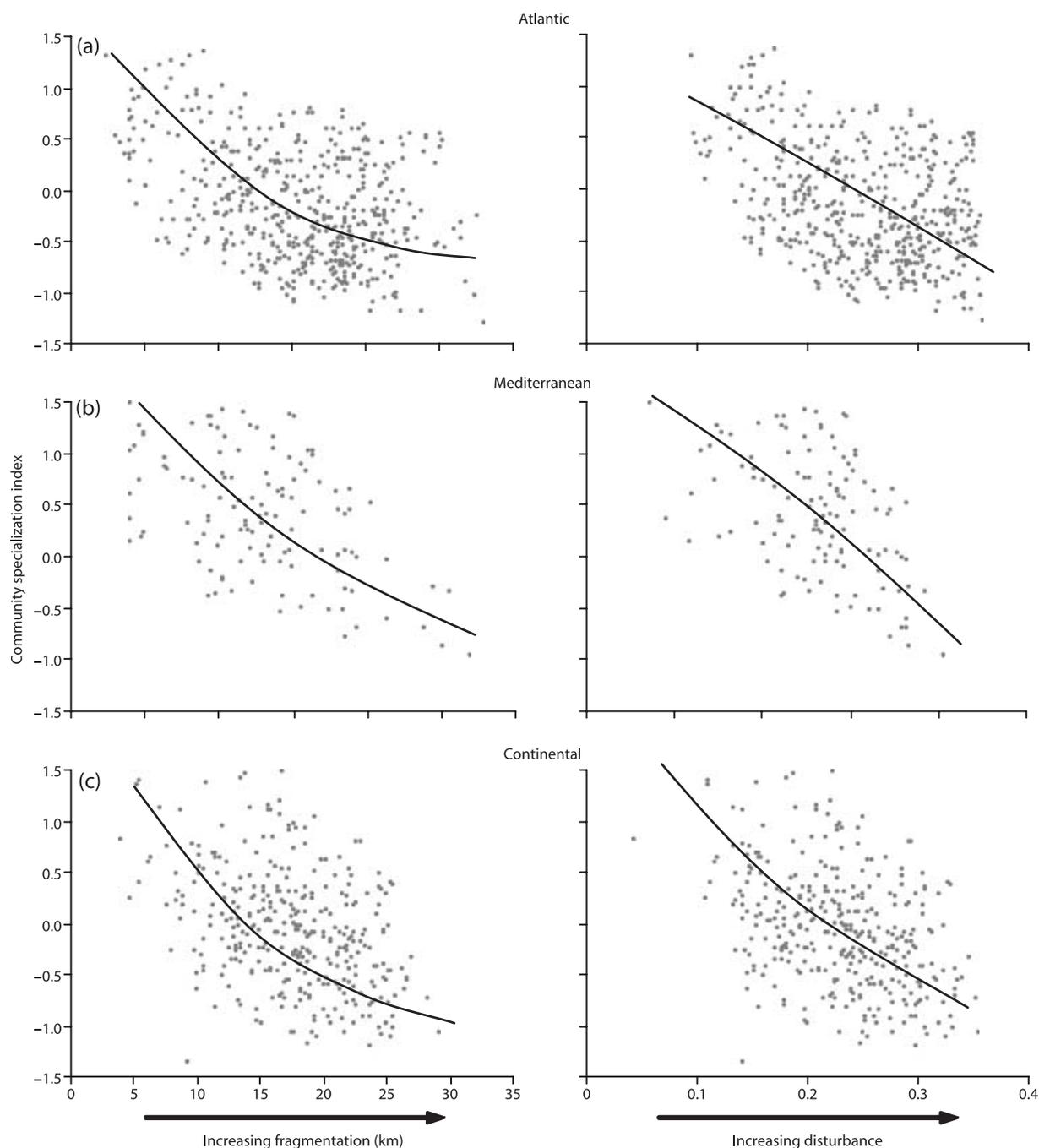
Figure 4 Relationships between the community specialization index (CSI) and sources of habitat degradation within each biogeographical zone. The relationships between CSI and fragmentation (in km) or disturbance are tested using respectively BBS plots monitored in (a) Atlantic ($n = 517$), (b) Mediterranean ($n = 151$) or (c) the Continental zone ($n = 360$) and accounting for habitat type (habitat was taken as a factor in the models). Smoothed curves are obtained with generalized additive mixed models (GAMMs) taking spatial dependence between samples into account.

types and biogeographical zones. These results emphasize that where the goal is to obtain an understanding of a community's fate in relation to large-scale environmental gradients, measuring CSI provides a sensitive and robust indicator.

Using SSI, all species were assigned a SSI value which reflected the strength of their habitat dependence while remaining entirely independent of their ecology and habitat preferences. For instance, the black woodpecker (*Dryocopus martius*), a forest specialist, had a SSI value of 1.235, which was closely followed by the house sparrow (*Passer domesticus*) (1.251), a human specialist species. At the community level, the average of SSI values calculated by considering all individuals recorded at a particular site is a

direct measure of the community tolerance at that site. This principle can be applied to all kinds of habitats, scales and organisms, without reliance upon a selected subset of species.

Various other measures could also be used to calculate a CSI: the key idea is to rank all species according to a specific functional trait which can be considered as a measure of niche breadth. For instance, a quantification of species performance, derived from the processes of acquiring, allocating and spending energy (which are connected to the physical environment) could also be used as a relevant functional trait to compute a CSI (McGill *et al.*, 2006).

Interestingly, in some cases we found curvilinear relationships between CSI and fragmentation (or disturbance). The nonlinearity in these patterns may be explained by the fact that edge length is a nonlinear function of habitat loss and attains maximum values with moderate levels of habitat loss and fragmentation (Fahrig, 2003). Alternatively, it is likely that many fragmented landscapes enclose old and stable fragments, in some cases allowing specialists to colonize and prosper in the residuals fragments. Further research on how specialist species and CSI respond to ancient or recent fragmentation (e.g. in working on fragments of different age), could thus help to refine our findings.

Moreover, the requirement by many species for multiple habitats suggests that their conservation is most effective in a mosaic environment (Law and Dickman, 1998). Anthropogenic activities transform ecosystems at many levels, which are likely to lead to a homogenization of habitat structure and composition. For instance, urban sprawl brings redundant artificial infrastructures which tend to homogenize urban-dominated landscapes (McKinney, 2002). To assess the impacts of landscape homogenization on biodiversity we think that the concept of biotic homogenization could be useful if used at spatially and temporally explicit scales, and if the link between changes in taxonomic diversity and changes in functional diversity is investigated (Rooney *et al.*, 2007). Measuring which specialist and generalist species are affected by landscape homogenization (not only by fragmentation or disturbance) and whether CSI is affected should be a promising step.

Change in community richness and diversity (Sax and Gaines, 2003) as well as taxonomic homogenization are scale dependent (Rooney *et al.*, 2007). Therefore, taxonomic differentiation does not always reflect a conservation improvement (neither does an increase in species richness). In contrast, the fact that human-induced environmental changes act as a non-random filter, selecting generalist species best able to survive within modified ecosystems (Smart *et al.*, 2006) should be consistent across scales.

Yet we still do not know the expected CSI value for a non-degraded landscape or how CSI should vary across habitats. This lack of reference means that CSI values must be evaluated across comparable situations: the same site at different times or different sites sharing some characteristics. In particular, any comparison of the effects of fragmentation on CSI across habitat types (natural, artificial and farmland) is complicated by the fact that each habitat is characterized by a specific pressure, history and intensity. For instance, recent French landscape dynamics have been mainly driven by an increase in artificial features and a decrease in natural meadow as well as in other traditional farmland habitats (IFEN, 2005). These dynamics are very complex and scale dependent. Although the link between urban sprawl and biotic homogenization has recently been highlighted (McKinney, 2006; Devictor *et al.*, 2007), the effects of other changes in land use should also be precisely assessed.

Using CSI as a biodiversity indicator relies on the assumption that the presence of specialist species in a given site is a signature of the good integrity and health of that site. We anticipate some situations where such an assumption does not hold (e.g. highly specialist species surviving in highly disturbed habitats, Attum *et al.*, 2006). However, we believe that such exceptions will be far less numerous than for other indicators based on species richness and/or abundance of species. Indeed, numerous studies have shown that landscape degradation can be associated (at least temporarily) with increase in species richness, abundance or diversity index so that working on changes in these non-functional metrics can lead to misleading results (Van Turnhout *et al.*, 2007).

We showed that CSI revealed a strong community response to large-scale habitat fragmentation and landscape disturbance, regardless of the habitat type or biogeographical zones considered. Most indicators quantifying the impacts of human pressures on biodiversity that are likely to be available in the near future (e.g. to assess the 2010 target), will be based upon existing data bases and monitoring schemes (Balmford *et al.*, 2003). The CSI is readily adaptable and can already be calculated in many cases from such data sources regularly involved in macroecological investigations. Trends in CSI are connected with the ecological niche theory, which renders CSI values easily interpretable and valuable for testing scientific predictions. Moreover, we tested relationships between CSI and habitat fragmentation or disturbance on birds, but our approach is flexible enough to be applicable to any organism at any spatial or temporal scale.

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BIOSKETCHES

Vincent Devictor has done his PhD on large-scale patterns in ecology. He is particularly interested in community ecology and in the functional homogenization process.

Romain Julliard and **Frédéric Jiguet** are research scientists developing conceptual and practical tools with the French Breeding Bird Survey. They work on topics ranging from the impact of global warming on birds to theoretical aspects of specialization.

Joanne Clavel is undertaking a PhD with the Conservation Group in Paris and is interested in specialist versus generalist behaviour. Current projects involve phylogenetic comparative methods to understand the evolution of specialization.

Alexandre Lee is a physical geographer interested in spatial analysis and cartography. He recently focused on the development of indicators describing landscape dynamics in France.

Denis Couvet is Professor at the Museum National d'Histoire Naturelle in France, and the director of the Conservation Group in Paris (CERSP). He is interested in genetic and evolutionary biology and various aspects of conservation biology.

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