Toward more concern for specialisation and less for species diversity in conserving farmland biodiversity

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ABSTRACT

In order to face the large and worrying biodiversity decline in agricultural landscapes, important policy instruments like agri-environmental schemes (AES) have been implemented. Studies that have examined the ecological effects of AES are now numerous and generally use indicators of biodiversity such as species richness and diversity as well as species abundance. Yet, it has been shown that simple metrics such as species richness or abundance may give misleading messages about biodiversity status and fate. Moreover, those indicators cannot detect another important source of biodiversity loss, biotic homogenisation. In this context, taking into account to a wider extent ecological difference among species would be more relevant, as well as focusing on the species specialisation which is known to be linked to higher species vulnerability. A bibliographic review investigating the criteria generally used to assess the success of AES showed that 55% of studies used species richness and/or abundance exclusively without any consideration of specialisation or other ecological traits in their evaluation of AES effectiveness. Based on data from the French breeding bird survey and studies at regional scale in France on farmland birds, we show that: (i) species richness and specialisation are generally negatively correlated in agricultural areas, (ii) habitat heterogeneity does not benefit specialist species, and (iii) monitoring of species diversity should be coupled with the monitoring of specialist species to improve conservation strategies in farming systems. Overall, this study emphasizes the need to account for both community richness and composition when assessing AES or similar conservation planning.

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1. Introduction

The evidence of the drastic decline in farmland bird populations has alarmed people and politicians to such a degree that conservation programmes have been promptly implemented in order to reverse these trends (Vickery et al., 2004). The most important policy instruments to protect biodiversity in agricultural landscapes are currently agri-environmental schemes (AES) (EEA, 2004; Kleijn et al., 2006). Other tools exist, like Natura 2000 (Visser et al., 2007) or protected areas (Gaston et al., 2006), but they are not exclusively dedicated to agricultural areas. AES aim at counteracting the negative effects of modern agriculture on the environment by providing financial incentives to farmers for adopting more environmentally friendly practices. All member-countries of the European Union (EU) are currently obliged to develop and implement AES, and investments in AES are substantial (Kleijn et al.,

2006). Not all AES schemes are dedicated to biodiversity conservation, but this is one of their multiple objectives, and a significant number of European AES specifically address this goal (Kleijn and Sutherland, 2003). Many studies have examined the ecological effects of AES, mostly using basic indicators of biodiversity such as species richness and diversity as well as species abundance (e.g. Weibull et al., 2003; Feehan et al., 2005; Roschewitz et al., 2005; Schmidt et al., 2005; Knop et al., 2006; Roth et al., 2008). There are several reasons for adopting such biodiversity indicators: (1) they are easy to measure, (2) they are commonly seen as a good proxies for biodiversity and ecosystems health and, (3) they are the most popular and widely-used measures of biodiversity.

However, from a conservation perspective, using these indicators can provide misleading messages about biodiversity's fate (Devictor and Robert, 2008) and may have poor ecological relevance (Washington, 2003). In particular, predictions about how species richness is expected to increase or decrease following fragmentation and disturbance often differ according to the time-scale and the habitat considered (Helm et al., 2006; Kimbro and Grosholz, 2006). Other measures of diversity (such as Shannon's diversity index) are also widely used, but were quickly proved to

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be misleading in many cases (Hurlbert, 1971). Besides, such diversity metrics have also been considered insufficiently informative and powerful when assessing AES effectiveness (Jeanneret et al., 2003). More importantly, high local diversity is not necessarily linked to conservation improvement, but it can result, instead, from biotic homogenisation (Van Turnhout et al., 2007), and thus lead to a global or local decrease of diversity (Olden and Rooney, 2006; Smart et al., 2006). In fact, the relevance of a given biodiversity metric depends mostly on the question being addressed. In the case of assessing conservation targets, one should ideally be able to link identified pressures of biodiversity loss to the trend of the metric considered.

In this respect, classifying biodiversity loss according to the two following types can be useful. First, biodiversity loss can refer to any impoverishment of local biodiversity which implies the decline of all or of a part of the community. Such biodiversity loss can be measured thanks to simple metrics such as diversity, species richness, biomass, abundance. Second, biodiversity loss can refer to the loss of regional diversity if some species (losers) are systematically replaced by other species (winners), a process coined biotic homogenisation (BH) (McKinney and Lockwood, 1999; Olden and Rooney, 2006; Smart et al., 2006; Devictor et al., 2008b). BH is a source of biodiversity loss which cannot be detected by simple diversity metrics or abundance; it represents the species and/or ecological traits which have been gained or lost following changes in community composition. To our knowledge, BH has been an overlooked aspect of biodiversity loss when assessing AES effectiveness.

In this context, taking into account to a wider extent ecological difference among species would be a simple way to estimate community response to disturbances (Devictor and Robert, 2008) such as intensive farming practices. In particular, ordering species along a generalist/specialist gradient could be useful (Julliard et al., 2006). Using niche breadth (i.e. a measure of species specialisation) was indeed shown to be a valuable predictor of species responses to habitat alteration (Warren et al., 2001; Swihart et al., 2006; Devictor et al., 2008a). Moreover, some recent studies have presented evidence linking anthropogenic disturbance and change in community composition in terms of specialist vs. generalist species at large spatial scale (Devictor et al., 2008a,b), but also at local scale and in response to farming practices (Aviron et al., 2005; Schweiger et al., 2007; Filippi-Codaccioni et al., 2009).

Finally, farming intensification has changed the agricultural landscape environment in many respects, from the increased use of fertilisers to the disappearance of uncultivated field margins and to more homogeneous landscapes (Berendse et al., 2004). Therefore, another aim of AES is to increase landscape heterogeneity, a common wisdom which has been supported by many studies (Benton et al., 2003; Roschewitz et al., 2005; Tscharntke et al., 2005; Rundlöf and Smith, 2006; Holzschuh et al., 2007). However, given that specialist species fitness is greater in a specific habitat type whereas generalists can thrive in a number of habitats, it is questionable whether such measures ultimately benefit specialist species and really help to prevent biotic homogenisation.

First, we present a bibliographic review of studies which assessed AES effectiveness for various taxa, focusing on the biodiversity metrics used in these studies. Then we used data from the breeding bird survey and another more local study on birds in France to investigate the link between the most used indicators and specialisation. Our aim was to assess the relationship between diversity metrics and community specialisation and how they can be used to improve conservation strategies in farming systems. Finally, we also used those two-dimensional studies in order to investigate the relationship between habitat heterogeneity and community specialisation.

2. Methods

2.1. Biodiversity indicators used to assess AES effectiveness

In order to assess which biodiversity indicators are commonly used when testing AES effectiveness, we performed an exhaustive review of published studies on this topic. For this, we used the Web of Knowledge (Thomson Reuters), which includes many scientific citations databases such as the Web of Science. This research was based on the word "agri-environment" in the title and as main topic (note that we only included studies published before 2009). Out of the 331 available records, closer inspection revealed that 91 were actually investigating AES and had used explicit indicators for that purpose. We then classified these indicators as follows: "Specialist/function", if the metric explicitly referred to the specialisation concept, functional traits or to the rare/common species classification; "SR/diversity", for species richness and diversity index; "Abundance" (number of individuals or similar measures, e.g. biomass); "Composition" (use of statistical analyses on species assemblages), "Demographic parameters" (use of indicators related to demographic parameters, e.g. reproductive success, survival rates), "Behaviour" (quantification of behaviour types, e.g. feeding rates, mobility); "Conservation status" (whole or part of the investigation on species of conservation concern, e.g. declining species, Red-Listed species); "Other" (other indicators, e.g. composite index based on multi-disciplinary study) (Supplementary materials 2 and 3 for reference list). When one of these indicators was used in a study, it was counted (Supplementary material 3). A single study could include more than one indicator. We compared indicators used between studies within different ecological groups used for evaluation (Supplementary material 3). Studies which focused on species of conservation concern or compared some of those with other less concerned species, for example, were all noted equally as using the "Conservation status indicator" (Supplementary material 3). However, as the knowledge of conservation status of species appears to vary according to the taxon considered (generally decreasing with the trophic level), due to the feasibility and existence of large-scale monitoring surveys, the proportion of studies using "Conservation status" as indicator was excessively high among the ecological groups considered. For example, farmland birds are all known as of conservation concern and all the studies of this group are noted as using this indicator.

2.2. Species richness vs. specialisation

As an indicator usefully complementing the general measures of species richness and diversity, we used the community specialisation index (CSI) which reflects, for a given community, the average specialisation level of species present in that community (following Julliard et al., 2006). To calculate CSI, we used the degree of habitat specialisation for a given species (species specialisation index (SSI)), which was quantified as the coefficient of variation (SD/mean) of its densities across habitats (using the 18 habitat classes recorded by observers of the French breeding bird survey (FBBS) during point counts) (see Julliard et al., 2006 for more details). The CSI was then calculated for each community as the average specific specialisation index of all individuals detected. CSI in plot j was thus given by:

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

where N was the total number of species recorded, a_{ij} the abundance of individuals of the species i in plot j, and SSI_i its specialisation index (Devictor et al., 2008b).

We then investigated the relationships between CSI and species richness at regional and national scales. To do so, we first used data from a published study on the regional impact of urbanisation on farmland bird specialists (see Filippi-Codaccioni et al., 2008). The study involved a species pool of 21 farmland birds determined in Filippi-Codaccioni et al. (2008) for which SR and CSI were

Table 1
Summary table of the indicators used in 91 published studies assessing AES benefits for biodiversity until 2008.

Group	Specialist/function	Conservation status	SR/diversity	Abundance	Composition	Demographic	Behaviour	Other	Number of studies
Vertebrates									
Mammals	0	2	2	3	0	1	0	1	4
Amphibians	0	0	1	1	0	0	0	0	1
Birds	8	22	6	23	1	5	2	0	27
Invertebrates									
Bumblebees	1	6	5	4	0	0	1	0	6
Butterflies	2	9	5	7	1	0	1	0	10
Carabid beetles	0	0	2	2	1	0	0	0	2
Soil macrofauna	2	0	2	2	1	0	0	0	2
Plants									
	3	1	7	4	1	0	0	0	9
Multiple trophic levels									
	6	7	22	17	8	2	2	1	30
Total (%)	24.18	51.65	57.14	69.23	14.29	8.79	6.59	2.20	100

Specialist/function = when study classifies species according to specialisation level, functional groups or rare/common category; Conservation status = when study investigates species of conservation concern (e.g. declining species, Red-Listed species); SR/diversity = when study uses species richness or species diversity index; Abundance = when study uses species or individuals number as well as similar measures (e.g. biomass); Composition = when study uses statistical analyses of species assemblages; Demographic = when study uses indicators related to demographic parameters (e.g. reproductive success, survival rates); Behaviour = when study quantifies one behaviour type (e.g. feeding, mobility); Other = when study refers to other indicators (e.g. composite index based on multi-disciplinary study).

Table 2
Classification of 43 farmland species according to their species specialisation index (SSI). Response to tree and bush presence (Bas et al., 2009) is given for each species.

SSI	Common name	Latin name	Rep-tree ± SE	Rep-bush ± SE
2.23	Northern Lapwing	*Vanellus vanellus*	0.06 ± 0.57	−0.46 ± 0.56
2.15	Zitting Cisticola	*Cisticola juncidis*	−0.37 ± 0.09	−0.31 ± 0.09
2.09	Yellow Wagtail	*Motacilla flava*	−0.53 ± 0.09	−0.72 ± 0.10
2.00	Tawny Pipit	*Anthus campestris*	−0.64 ± 0.14	−0.27 ± 0.14
1.90	Stone-Curlew	*Burhinus oedicnemus*	−0.17 ± 0.23	0.12 ± 0.23
1.70	Northern Wheatear	*Oenanthe oenanthe*	−0.84 ± 0.32	−0.19 ± 0.34
1.52	Common quail	*Coturnix coturnix*	−0.28 ± 0.12	−0.05 ± 0.12
1.48	Marsh Warbler	*Acrocephalus palustris*	−0.07 ± 0.50	0.24 ± 0.48
1.46	Corn Bunting	*Emberiza calandra*	−0.48 ± 0.08	−0.22 ± 0.08
1.46	Whinchat	*Saxicola rubetra*	−0.04 ± 0.26	−0.31 ± 0.25
1.39	Fieldfare	*Turdus pilaris*	0.50 ± 0.38	−1.38 ± 0.37
1.37	Meadow Pipit	*Anthus pratensis*	−1.26 ± 1.50	−0.82 ± 1.60
1.36	Cetti's Warbler	*Cettia cetti*	0.51 ± 0.23	0.24 ± 0.20
1.34	Woodchat Shrike	*Lanius senator*	−0.08 ± 1.30	0.12 ± 1.20
1.32	Ortolan Bunting	*Emberiza hortulana*	0.62 ± 0.34	−0.57 ± 0.31
1.31	Wryneck	*Jynx torquilla*	0.53 ± 0.23	0.17 ± 0.20
1.25	Hen Harrier	*Circus cyaneus*	−0.43 ± 0.30	−0.10 ± 0.31
1.25	Common Whitethroat	*Sylvia communis*	−0.10 ± 0.19	−0.20 ± 0.18
1.24	Red-backed Shrike	*Lanius collurio*	0.03 ± 0.13	0.37 ± 0.12
1.16	Skylark	*Alauda arvensis*	−0.39 ± 0.04	−0.37 ± 0.04
1.01	Lesser Whitethroat	*Sylvia curruca*	−0.01 ± 0.14	0.70 ± 0.15
0.91	Tree Pipit	*Anthus trivialis*	0.40 ± 0.08	0.11 ± 0.07
0.90	Wood Lark	*Lullula arborea*	0.24 ± 0.08	−0.07 ± 0.07
0.85	Rook	*Corvus frugilegus*	−0.21 ± 0.28	−0.49 ± 0.29
0.78	Stonechat	*Saxicola torquata*	−0.06 ± 0.07	0.04 ± 0.06
0.75	Black Kite	*Milvus migrans*	−0.15 ± 0.23	−0.35 ± 0.22
0.72	Melodious Warbler	*Hippolai's polyglotta*	0.16 ± 0.07	0.56 ± 0.07
0.71	Yellowhammer	*Emberiza citrinella*	0.18 ± 0.06	0.33 ± 0.05
0.70	Goldfinch	*Carduelis carduelis*	0.09 ± 0.07	0.14 ± 0.07
0.70	Linnet	*Carduelis cannabina*	0.04 ± 0.11	−0.14 ± 0.11
0.69	Garden Warbler	*Sylvia borin*	0.22 ± 0.09	0.48 ± 0.09
0.69	White Wagtail	*Motacilla alba*	0.12 ± 0.08	−0.22 ± 0.08
0.68	Kestrel	*Falco tinnunculus*	0.15 ± 0.11	−0.09 ± 0.10
0.65	Common Whitethroat	*Sylvia communis*	0.04 ± 0.06	0.52 ± 0.06
0.61	Hoopoe	*Upupa epops*	0.44 ± 0.12	0.00 ± 0.11
0.59	Cirl Bunting	*Emberiza cirlus*	0.23 ± 0.09	0.30 ± 0.08
0.57	Common Starling	*Sturnus vulgaris*	0.26 ± 0.10	−0.05 ± 0.09
0.49	Buzzard	*Buteo buteo*	0.03 ± 0.10	0.19 ± 0.10
0.47	Rufous Nightingale	*Luscinia megarhynchos*	0.22 ± 0.05	0.47 ± 0.05
0.44	Crested Lark	*Galerida cristata*	−0.72 ± 0.16	−0.37 ± 0.17
0.40	Turtle Dove	*Streptopelia turtur*	0.11 ± 0.06	0.38 ± 0.06
0.38	Green Woodpecker	*Picus viridis*	0.38 ± 0.08	−0.03 ± 0.07
0.28	Carrion crow	*Corvus corone*	0.14 ± 0.07	−0.08 ± 0.07

calculated (for the present study purpose) in each of the 92 1×1 km squares of a fictive grid built using the geographical information system (GIS) covering the entire Seine-et-Marne region (5915 km^2), France. Those squares were chosen primarily in function of their different levels of urbanisation (which was the subject of Filippi-Codaccioni et al. (2008) study). We took this varying degree of urbanisation into account when assessing the relationship between CSI and SR (ANOVA (type II error)).

At national scale, we investigated the same relationship by using FBBS data from 2001 to 2007. A mean species richness and a mean CSI were calculated for every 2×2 km square monitored by the FBBS categorised by observers as agricultural habitats ($n = 861$) for this period.

For both studies (i.e. regional and national), bird abundance was sampled using the point count method. Each 1×1 km square was sampled with five point counts conducted exclusively in farmland habitat for the study at regional scale, while at national scale, 10 point counts were carried out. For each point count, every bird seen or heard was recorded during 5 min exactly. Each point was visited twice (once before and once after the 8th May with a 4 week interval). In each study, for a given species at a given point, we recorded the maximum number of individuals counted between the two visits (see Supplementary materials 1 as well as Filippi-Codaccioni et al. (2008) and Julliard et al. (2006) for more details about the regional and national survey, respectively).

2.3. Specialisation and habitat heterogeneity

In addition to the relationship between CSI and species richness presented above, we also used a species-based approach to explore the relationship between farmland bird species responses to habitat diversity and their specialisation (SSI) in agricultural areas. This relationship was also investigated at regional and national scale in France.

At regional scale, we used data from Filippi-Codaccioni et al. (2009), a study based on the same species pool of 21 farmland birds, but in which species abundance was related to different farming systems. In this study, authors used multiple regression modelling to relate species abundance to farming practices, which accounted for many variables concerning landscape and field structure and composition. The purpose of the authors was to investigate whether species specialisation could explain abundance variations between farming systems. They extracted species responses to farming systems from this model in order to relate it to SSI in a second model (see Supplementary material 1 and/or Filippi-Codaccioni et al. (2009) for complete methodological details). Here, our interest was rather to focus on whether specialisation level could determine abundance variations along a gradient of landscape heterogeneity measured with the Shannon's diversity index (SDI) (Supplementary material 1). Therefore we only extracted species responses to SDI, a common and very often used measure of landscape diversity, from the model used in Filippi-Codaccioni et al. (2009), and then related these responses to SSI in a second model. In doing so, we were able to determine whether the most specialised species were more affected by habitat diversity than less specialised species. SSI values for each species (Julliard et al., 2006) were the same as in the Filippi-Codaccioni et al. (2009) study. Each species' response estimate was weighted by the inverse of its variance when responses were modelled in function of SSI (see Filippi-Codaccioni et al., 2009, and/or Supplementary material 1 for detailed methods).

Another important component of landscape diversity which could be associated with more local diversity is the composition of field edges. In arable landscapes, field edges can even represent the major source of heterogeneity in landscape composition and structure. As the management and even the introduction of vertical features such as trees or hedges are often proposed in AES options, it seemed relevant to investigate the responses of specialist species to those features. For this, we made use of a recent study conducted at national scale, which aimed at testing the response of different nesting strategies to those features and to farming intensity. For that purpose, local abundance of 43 farmland bird species was modelled using a multiple regression, with production intensity (PI) as an independent variable associated with variables controlling for potential habitat and climate effects:

$$\text{Abundance} \sim F_1 + F_2 + \cdots + F_{11} + C_1^2 + C_1 + C_2^2 + C_2 + C_3^2 + C_3$$
$$+ C_4^2 + C_4 + \text{TP} + \text{SP} + \text{PI},$$

where F represents 11 farmland habitat frequencies, C four climatic variables (Jiguet et al., 2007; Bas et al., 2009), TP tree presence/absence, SP shrub presence/absence and PI a production intensity index (Bas et al., 2009).

As we are interested here in testing the relationship between the responses (variation in abundance) of farmland bird species to the presence of trees and bushes (natural hedges or not), we extracted them from this model and correlated them to SSI (Table 2), (see Bas et al. (2009) and/or Supplementary material 1 for more details on the methods).

Note that although we used data from studies already published, we focused on new relationships which have never been explored previously. All calculations were performed using the statistical software R 2.7.1 (R Development Core Team, 2007).

3. Results

3.1. Biodiversity indicators used to assess AES effectiveness

The most often used indicator was species abundance (69%), immediately followed by SR and species diversity (57%) (Table 1). The studies (23%) used SR/diversity or/and Abundance as indicators exclusively, while 10% used SR/diversity alone and 2.2%
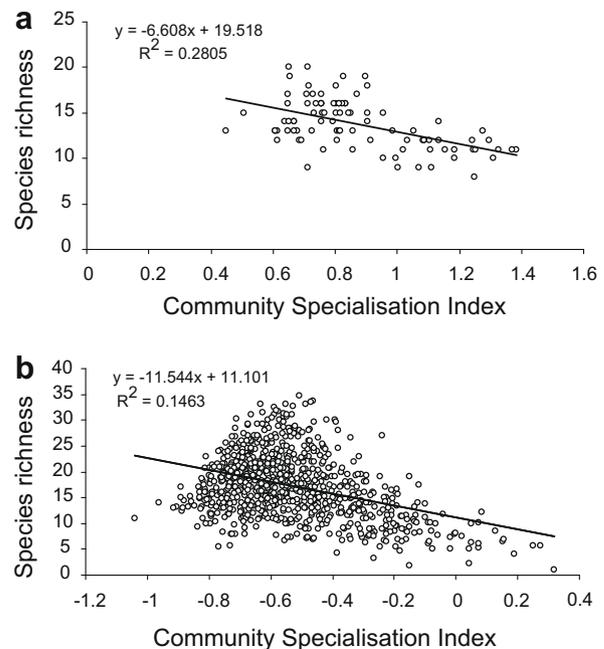

Fig. 1. Relationship between farmland bird species richness and the community specialisation index (CSI) of farmland bird communities in agricultural areas (a) at a region scale and (b) at national scale in France.

used Abundance alone. 24% of studies took species traits or specialisation into consideration when assessing AES effectiveness to promote biodiversity. About half of the studies (52%) dealt with species of conservation concern or considered some of them in their analyses (Table 1). The highest proportion of those studies consisted of studies concerning farmland birds and pollinators, as many of them are recognised as declining species. Overall, regardless of any considerations of conservation status (which is a function of scientific knowledge based on large-scale monitoring surveys, and varies between taxa), 55% of studies used SR/diversity and/or Abundance alone. 53% and 40.65% of the studies used Abundance and SR/diversity without any classification into functional or ecological groups, respectively. Comparing studies on

plants, pollinators and birds, we found that the higher proportion of studies using Abundance and/or SR/diversity alone (without any other indicators but not taking into account conservation status) could be attributed to studies on pollinators (80%), followed by studies on plants (56%) and birds (52%), while studies using various ecological groups used those indicators alone in 49% of the cases.

3.2. Species richness vs. specialisation

At regional scale, a significant linear negative relationship was found ($F_{1,89} = 15.85$; $P < 0.001$) meaning that specialisation and SR were negatively correlated (Fig. 1a) in farmland bird communi-
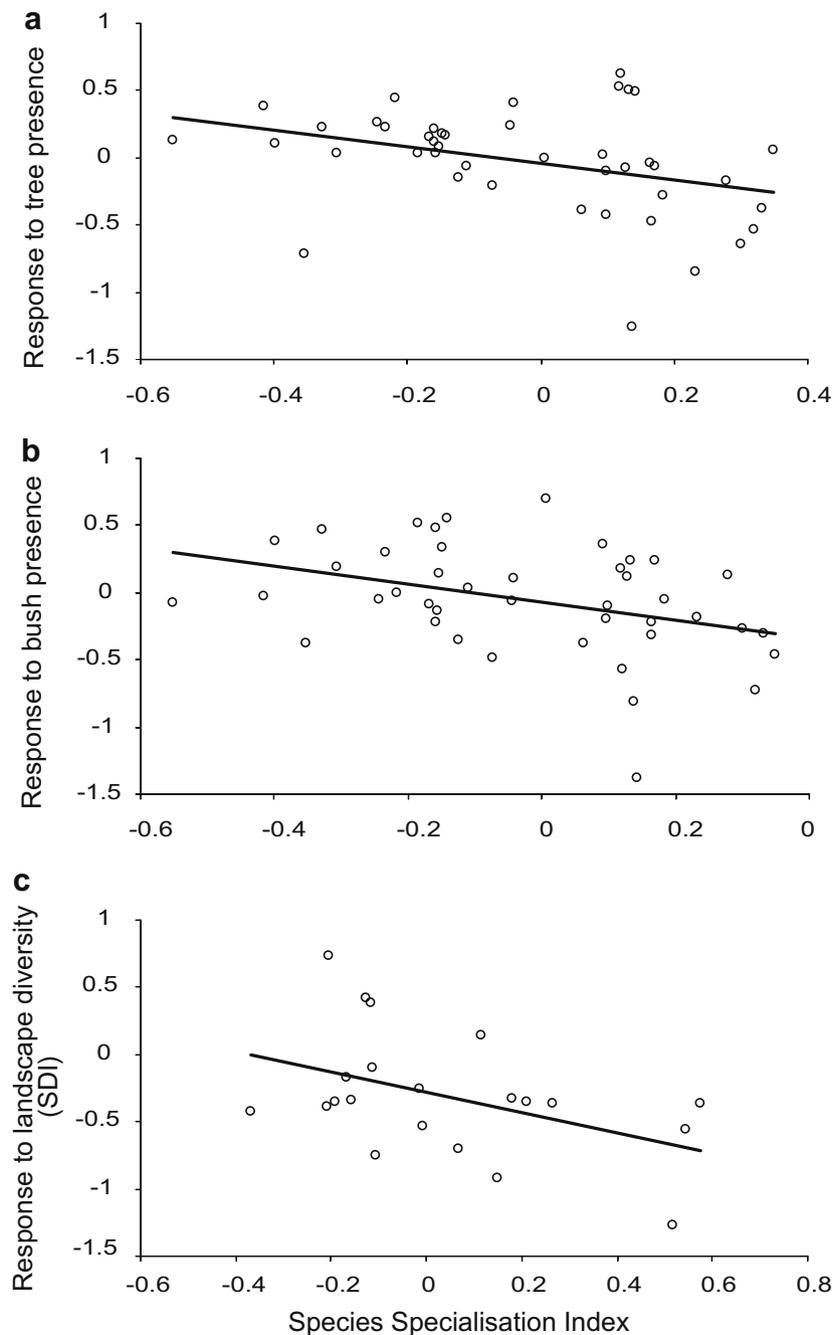
Fig. 2. Relationship between 43 farmland species responses (in terms of abundance) and the presence of trees (a) and bushes (b) within 100 m of a French breeding bird survey point count and the species specialisation index (SSI) (Julliard et al., 2006); (c) represents the relationship between abundance responses of 21 farmland species and the Shannon's diversity index (SDI) and the SSI.

ties. At national scale, a negative correlation was also found between farmland bird specialisation and SR ($r = -0.38$, $P < 0.001$) (Fig. 1b).

3.3. Specialisation and habitat heterogeneity

At national scale, a negative relationship was found between the abundance of the most specialised farmland species and habitat diversity (Fig. 2a; presence of trees: $F_{1,41} = 32.12$, $P < 0.001$; Fig. 2b; presence of bushes: $F_{1,41} = 13.35$, $P < 0.001$; Table 2). Such a relationship was not significant for farmland birds at local scale in the study concerning the Seine-et-Marne region (Fig. 2c; SDI: $F_{1,41} = 2.49$, $P = 0.13$).

4. Discussion

4.1. Biodiversity indicators used to assess AES effectiveness

We found that the most commonly used indicator was Abundance (number of individuals or similar measures) (69%), immediately followed by SR and species diversity (57%). More importantly, 23% of studies used either Abundance and/or SR as indicators exclusively and 53% of the studies used Abundance without any classification into functional or ecological groups. Yet, the relevance of using richness and diversity metrics, or abundance as proxies for reflecting community status has been questioned (Washington, 2003; Kinzig et al., 2002; Devictor and Robert, 2008). These indices can indeed show confusing trends and have even provided misleading messages about the status of communities facing disturbances (Devictor and Robert, 2008). In contrast, reflecting the composition of the community in terms of habitat specialist and generalist species was found to be more robust and powerful to reflect disturbance effects (Aviron et al., 2007). However, we found that only 24% of studies considered species traits or specialisation when assessing a biodiversity gain. Moreover, some studies made use of certain classifications (e.g. guilds) without any explanation about their possible relationship with conservation issues.

Although the extent of the use of species richness as an indicator is less worrying than expected (10% of exclusive use), the fact that abundance of individuals is so often used as the only other criterion in studies is not very encouraging. Because of the possible different messages these indicators can give, and of their inability to measure biological homogenisation, we recommend using concomitantly other indicators such as specialisation or other species' characteristics linked to their ecological roles. However, most of these studies are either done on ecological groups of conservation concern (like farmland birds or pollinators) or consider the response of Red-Listed or declining species when assessing AES effectiveness, which gives a conservation value to these studies. Unfortunately, this does not provide any information about possible functional homogenisation.

Many authors explained their use of species richness as an indicator when assessing AES effectiveness by the relationship found between it and ecosystem functioning (Weibull et al., 2003; Tscharntke et al., 2005). However, Diaz and Cabido (2001) showed in their review that there was a growing consensus that the effects of diversity on ecosystem processes should be attributed to the functional traits (value and range) of individual species and their interactions rather than to species number per se (Diaz and Cabido, 2001). They also demonstrated that SR should not be a substitute for functional richness.

We thus think that a greater use of specialisation measures to detect priorities for conservation at the species and community le-

vel should be recommended. They should complement SR and abundance indicators in AES implementation and evaluation.

4.2. Species richness vs. specialisation

Modelling studies have shown that SR and specialisation measures can show contrary trends (Devictor and Robert, 2008). Here, we have shown that – for birds – this can also be the case in agricultural areas, regardless of spatial scale. We found a negative correlation between species richness and community specialization index (CSI), suggesting that preserving communities on the basis of species richness does not generally benefit specialist species. Beyond this relationship, one may ask whether species richness and CSI are good indicators for communities considered as negatively impacted by farmland intensification. We therefore devised an alternative model to refine our findings, using the proportion of declining species as the independent variable, with SR and CSI as explanatory variables, and allowing an interaction between CSI and SR. The criterion for declining farmland species in France was the species trends calculated from the FBBS data since 1989–2007 (Jiguet et al., 2007). We found that the proportion of declining farmland species was positively related to species richness ($F_{1,843} = 40.54$; $P < 0.001$). We also found that communities holding more specialised species (i.e. with high CSI) were those with a higher proportion of declining farmland birds ($F_{1,843} = 37.64$; $P < 0.001$). Finally, the interaction between CSI and species richness was also related to the proportion of declining species ($F_{1,841} = 4.90$; $P = 0.02$; $r^2 = 0.14$ for the whole model).

These additional results suggest complex relationships between species trends, community richness and composition: while the proportion of declining species is positively correlated to species richness and CSI, CSI is negatively correlated to species richness. Regardless of the mechanism explaining these patterns (this would require further investigations, which are beyond the scope of this paper), these results suggest that community richness and composition should be considered together when searching for optimal conservation planning. Indeed, for a given level of species richness, focusing on more specialised communities will optimise conservation targets. Similarly, for a given level of specialisation, increasing the number of species will optimise conservation strategies. However, how representative these results are for other species groups or other regions is open to debate. For example, some species-rich plant communities could host a large proportion of specialist plant or arthropod species (Suutari et al., 2009). We therefore must extend our research to other taxa before generalising.

Interestingly, our results also echoed those of other authors on the negative relationship between rarity and species diversity (i.e., common species and rare species were found in rich vs. poor communities respectively, Lennon et al., 2004; Šizling et al., 2009). We think that our results could be driven by the same phenomenon of negative relationship between specialisation and species richness. However, to describe which ecological processes are driving this pattern, one should have a clear definition of what is meant by "rarity". Following Rabinowitz (1981), we think that rarity is multifaceted and depends on (i) species range, (ii) local species abundance, and (iii) resource distribution. Interestingly, authors have mainly focused on rarity using one specific definition (generally the species range) but the relation between specialisation and the combination of different forms of rarity has yet to be explored. It could be possible that specialisation may be a better predictor of SR than the other components of rarity (local abundance, continuity of distribution). It would therefore be very interesting to explore this perspective with further analysis, requiring further theoretical and macro-ecological development beyond the scope of our paper.

4.3. Specialisation and habitat heterogeneity

A recent review argued for a landscape perspective in the biodiversity enhancement of farmland ecosystems (Tscharntke et al., 2005). The authors' arguments were that landscape complexity may compensate for biodiversity loss because of local management intensity. One of their examples was taken from Roschewitz et al. (2005), in which the species diversity of arable weeds was found to be higher in organic than in conventional fields, but only in homogenous landscapes. Similar evidence has also been found for other taxa (Rundlöf and Smith, 2006; Holzschuh et al., 2007).

In the light of our results, we suggest that caution should be used when assessing the effectiveness of conservation plans based on greater landscape heterogeneity. First, the species trait approach is often ignored in those kinds of study. Yet the effect of landscape heterogeneity on species abundance is different for specialist and generalist species. For instance, Filippi-Codaccioni et al. (2009) found that the abundance of specialist bird species was higher in organic fields than in conventional ones regardless of the landscape diversity. It is possible that the study of Filippi-Codaccioni et al. (2009) did not cover the entire gradient from cleared to complex landscapes; nevertheless, structural and compositional changes between landscapes were very important.

Moreover, other studies found that arable fields in high intensity agricultural landscapes with little non-crop area can support a similar diversity of cereal aphid parasitoids as structurally complex landscapes (Vollhardt et al., 2008). The authors concluded that aphid parasitoids may find necessary resources even in simple landscapes, making generalisations concerning the relationship between landscape composition and biodiversity in arable fields difficult (Vollhardt et al., 2008).

Finally, the analysis we conducted in this study showed mainly a negative relationship between abundance of most farmland specialist species and habitat diversity. We believe that this evidence must be taken into account in the frame of this landscape composition/biodiversity debate. Moreover, these results suggest that current AES which encourage habitat diversity through vertical features enhancement could affect negatively the most vulnerable species (the most specialised ones). One issue which might deserve some discussion in relation to the bird results in this paper is the potential differences in the spatial scale at which birds vs. plants and insects respond to land use and habitat heterogeneity. It seems that some farmland specialist bird species really need relatively large open landscapes and can be harmfully affected by habitat heterogeneity such as trees and bushes. However, many (probably even most) other species are dependent on smaller patches of suitable habitat and are therefore much less likely to be affected by landscape level habitat heterogeneity.

These results hint at the general question about which kind of species we want to promote in which landscape, a question which arose from recent studies on AES (Vickery et al., 2004; Kleijn et al., 2006). As it is impossible to design measures which will benefit all species, making choices is inevitable. We suggest, as a minimum, that diversity metrics could be usefully coupled with more trait-based approaches when assessing conservation strategies.

5. Conclusion

We think that a greater focus on the specialisation character of species would improve the current frame of conservation actions in agricultural landscapes. Indeed, growing evidence indicates specialists as the most vulnerable species facing global changes and especially agricultural intensification. The use of species richness or abundance as cure-all indicators is not sufficient to detect possible biotic homogenisation. Moreover, we have shown that the habitat heterogeneity goal of many AES could mask negative effects on the most specialist bird species.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.03.031.

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