Community richness and stability in agricultural landscapes: The importance of surrounding habitats

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Abstract

In this paper, the role played by habitat diversity in the landscape on species richness and on the stability of farmland bird communities was investigated. Species richness was estimated on 374 samples monitored in farmland by the French breeding bird survey during the 2001–2005 period. A capture–recapture approach was used to estimate species richness accounting for the variation in detection probability among species of the 100 most common species detected in farmland. Landscape structure and composition were measured both in farmland and in adjacent habitats. The independent effect of each variable on community richness and stability was further assessed using hierarchical variance partitioning and taking spatial autocorrelation into account. A strong matrix effect was detected: non-cropped land deeply influenced richness and stability of bird assemblages.
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Keywords: Agricultural landscape; Bird; Breeding bird survey; Community dynamics; Detectability; Matrix effect; Spatial analysis; Mixed models

1. Introduction

The negative effects of landscape homogenization and agriculture intensification on biodiversity are recognized (Benton et al., 2003) and have been studied at many spatial scales on plants, invertebrates, and vertebrates (Stoate et al., 2001). Many studies have focused on birds as this taxonomic group provides good indicators of environmental changes since it is easily monitored, and high in the food web. Most of these studies have concluded that farmland species are in trouble (Donald et al., 2001). At the local scale, specific agricultural practices, such as the increased use of pesticide and inorganic fertilizers, were identified as plausible explanations for the decline in farmland bird populations (Chamberlain and Fuller, 2000; Newton, 2004). At the landscape scale, the structure and composition of the landscape matrix have been investigated theoretically and are expected to affect population dynamics (Andrén, 1994).

In particular, for a given habitat, the diversity of the surrounding habitats has been shown to deeply influence the community found within the given habitat, although this result differed according to the scale, the habitat and the group considered (Clergeau et al., 2001).

To assess the state of farmland birds, research on communities has principally focused either on farm-scale studies of local patterns or on broader scale relationships between birds and major climatic or land-use variables. Studies at an intermediate spatial scale employing sample plots of a few km^2 are far less common (Heikkinen et al., 2004). Yet, landscape variables of non-cropped surrounding habitats in agricultural landscapes are expected to play a major role in bird assemblage richness (Söderström and Pärt, 2000; Krauss et al., 2004). Indeed, in open and fragmented farmlands, landscapes often consist of two kinds of habitat. The first is the effectively cultivated habitat, where the agricultural practices and the size and structure of the farmland are major components explaining the fate of biodiversity (Selmi and Boulinier, 2003). The other is made up of the surroundings, such as patches of

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wetland, woodland, or human settlements. These non-agricultural patches may strongly affect farmland bird communities by providing breeding sites, food supplies, or by potentially allowing the colonization by individuals and species (Woodhouse et al., 2005; Buckingham et al., 2006).

Little attention has been paid to such matrix effects on organisms living in open habitats in which species may have high mobility and a generalized habitat use (Söderström and Pärt, 2000). Moreover, when communities were studied within complex landscapes, community composition was often only described in terms of observed species richness or abundance for target species, while the dynamic processes were rarely considered for the whole community (Chamberlain and Fuller, 2000; Bennett et al., 2004).

The aim of this study was to identify the relative effects of the landscape's structure and the composition of agricultural and non-agricultural habitats on species richness and community stability at a landscape scale, while accounting for heterogeneity in species detection and spatial autocorrelation. More specifically, a positive effect of either agricultural or adjacent habitat diversity on bird species richness was expected. Concerning community dynamics, species found in more diverse landscapes any given year should, on average, have a higher probability of still being present the following year. Negative effects of intensively farmed uniform landscape, such as reduced habitat hedges and low connectivity among diverse habitats should lead to an increase in community instability. Thus, the prediction of a higher temporal variability in bird communities in more homogeneous farmland landscapes was also tested.

2. Methods

The French breeding bird survey (BBS) is a standardized monitoring program in which volunteer skilled ornithologists identify breeding birds by song or visual contacts each spring. Each observer is allocated a locality, and a four km^2 plot to be surveyed which is randomly selected within a 10-km radius around this locality (i.e. among 80 possible plots). Such random selection ensures that the survey covers a representative selection of habitats (including intensive farmland, ordinary forest, suburbs and cities). Each plot is monitored twice in the spring, once before and once after the eighth of May, with 4–6 weeks between sampling events. In each plot, the observer carries out 10 evenly distributed point counts, within which the observer records every species heard or seen during a 5-min period. The same observer monitors the same plot each year (Julliard and Jiguet, 2002). In this study, all plots monitored during the 2001–2005 period, in which at least five points located in farmland (according to the habitat codes recorded by the observers in the field) were analyzed. The first five farmland point counts of each square were then selected (in order to compute community parameters with a constant sampling effort) and,

for each given point, counts of the two annual visits were summed. Species recorded at these point counts were mainly farmland bird specialist species. However, in order to extend the scope of the analysis to other species encountered in farmland, the 100 most common passerine and near-passerine bird species (from Columbiforms to Piciforms) detected by the BBS were considered. Therefore, many of the species considered may benefit from secondary habitats (hedges, bushes, buildings or small wetlands), but are not strictly linked with farmland.

The matrix of presence/absence of encountered species at each of the five point counts was processed each year to estimate species richness by running the COMDYN program (Hines et al., 1999). COMDYN's algorithm allows one to consider heterogeneous detection probability among species, using the capture–recapture model $M(h)$ and the associated jackknife estimator. This model was the most frequently selected model in the framework of species richness estimation for breeding bird survey data (Boulinier et al., 1998b; Jiguet et al., 2005). For each plot, species richness estimates were averaged over 2001–2005. Only plots for which there were more than two annual estimates of species richness were included in the analyses. Second, community stability for each BBS plot was expressed as the temporal variation in species richness (Boulinier et al., 1998a; Lekve et al., 2002; Newmark, 2006). The relative year-to-year variability in species' numbers was estimated using the coefficient of variation (CV) of species richness over 2001–2005 using variance estimates of annual species richness over that period, with an approach proposed by Link and Nichols (1994) that accounts for sampling variance. When available, the sampling variance which is induced by the sampling procedure (e.g. induced by heterogeneity in detection probability) can be subtracted from the raw variance estimate to get an estimate of the true process variance. Therefore, the average sampling variance associated with annual estimates of species richness (provided by COMDYN), was subtracted from the overall total variance (estimated over time using the point estimate of species richness). Community stability was thus the ratio of the square root of the estimated true temporal variance to the mean of the species richness estimate (Boulinier et al., 1998a). This community stability estimate was independent of the number of years considered for each plot (ANOVA, $F_{371,2} = 1.39$, $P = 0.24$) and not correlated to the mean of species richness ($r = 0.069$, $P = 0.18$).

Variables related to landscape features within each surveyed plot were obtained using the geographical information system package ArcView 3.2 (ESRI, 2000) and the Corine land cover database. The latter is a national geo-referenced database including the main habitats for the whole country in contiguous polygons classified according to 44 different land-cover categories (Bossard et al., 2000). BBS squares were overlaid on this independent land cover database and two groups of explanatory variables were built: habitat cover and landscape diversity variables (Table 1).

Table 1
Variables used to describe landscape attributes, built from the French Corine land cover database

Landscape attribute	Variable	Variable description
Landscape composition		
Agricultural	Intensive	Annual arable crops Irrigated cultures and vineyards
	Pasture	Uncultivated meadows
	Extensive	Mixture of annual crops and pastures
Adjacent	Forest	Coniferous and mixed forest
	Scrub	Natural grassland and bushy vegetation
	Artificial	Any human settlements and built-up areas
Landscape structure	Farmland diversity	Shannon's diversity index
	Surrounding diversity	Shannon's diversity index

More specifically, the 44 land-cover categories were grouped into six main habitat types in order to get landscapes composition variables which were both relevant to test predictions on bird community, and compatible with a landscape scale investigation. These six main habitat types could be subdivided into three agricultural habitats: (i) intensive agricultural land which included large open fields of annually harvested plants and irrigated cultures as well as permanent crops such as vineyards and olive groves; (ii) extensive agricultural land, which embodied small farmlands generally growing non-permanent crops (arable land or pastures) but associated with permanent crops on the same parcel. A significant areas of vegetation is generally associated with such heterogeneous farmlands; (iii) pasture, which was farmland used mainly for grazing but which could also be harvested mechanically. This pasture category included many areas with hedges. The other three non-farmland habitats were categorised as: (iv) forest, (v) scrub (which included natural moors and transitional woodland) and (vi) artificial areas (Table 1).

A landscape diversity variable was further measured for both farmland habitat and surrounding habitats using Shannon's diversity index. This farmland diversity index was calculated using all polygons of any habitat type related to farmland (among the 44 land cover categories) while surrounding diversity was calculated using all non-agricultural habitat types.

Statistical analysis was conducted in three steps. First, a semivariogram of each community parameter (species richness and stability) was plotted to describe spatial autocorrelation. Semivariograms were performed by summing up all the squared differences of the error values between each pair of points located at different distances, to measure the dissimilarity of the data points with distance. Different theoretical models were tested including linear, exponential, spherical, Gaussian and rational quadratic models and the best-fitting semivariogram and the

corresponding parameters (range and nugget) were selected (Fortin et al., 2002). Second, a hierarchical variance partitioning analysis was conducted in order to compute independent contributions of each landscape variable accounting for correlation between these variables (Mac Nally, 2002). However, hierarchical partitioning analysis cannot explicitly handle spatial autocorrelation structure. Therefore, to produce a summary autocovariate accounting for the spatial dependence for each community descriptor (richness and stability), the mean of each descriptor found in the neighboring area (i.e. in a distance equivalent to the range) of each sample was used in the hierarchical variance partitioning (Heikkinen et al., 2004). For each community parameter (richness and stability), Mac Nally's (2002) randomisation method was used (with 1000 simulations) to assess the statistical significance of the independent contribution of each predictor variable (including spatial autocovariates). Third, spatial parameters inherited from the fitted semivariogram, spatial coordinates of samples and environmental variables selected by hierarchical partitioning analysis were included in a final general least-square model (GLS) with each community parameter estimate as a dependant variable and landscape features as independent variables. All analyses were conducted using the nlme and hier.part packages of the R statistical software (Team, 2004).

3. Results

The semivariance of species richness increased with distance, indicating that observations were spatially correlated (Fig. 1a). The best fitted semivariogram was an exponential model with a range of 300 km and a nugget of 0.75. Thus, the part of variance attributed to spatial autocorrelation was 25% (1 − 0.75).

Hierarchical partitioning analysis showed that all variables except artificial areas, scrub and extensive farmland had independent explanatory power (Fig. 2a). An important amount of the explained variance was related to the joint effects of the variables. However, among landscape composition, intensive cover had the highest explanatory power (13.8%), and among landscape structure variables, farmland diversity had the highest independent contribution (15.7%). The autocovariate variable also had an independent significant effect suggesting that each BBS plot was not isolated but spatially dependant. The GLS mixed model using the four environmental variables with significant independent effect and accounting for spatial dependence between samples ($R^2 = 0.13$ for the entire model) further revealed that species richness was positively related to the diversity of farmland and surrounding habitats ($t_{368} = 3.45$, $P < 0.001$; $t_{368} = 2.49$, $P = 0.012$, respectively) but negatively related to intensive farmlands ($t_{368} = -2.80$, $P = 0.005$). No significant effect was detected for scrub and forest cover.
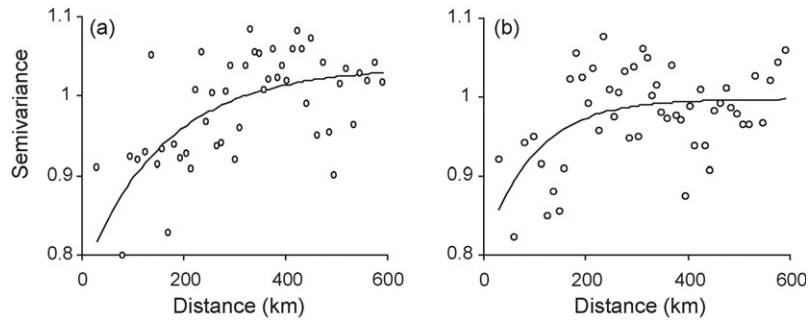
Fig. 1. Empirical semivariograms of each community parameter: (a) species richness; (b) community stability. The semivariogram values are calculated for pairs of standardized residuals between samples according to distance between samples.

The community stability estimate also had a clear spatial structure (Fig. 1b). The best fitting semivariogram was an exponential model with a range of 250 km and a nugget of 0.80. The part of variance attributed to spatial autocorrelation was thus 20%. Five variables had independent explanatory power (Fig. 2b). Artificial areas had the highest independent contribution among landscape cover (25%) and adjacent diversity among landscape structure (18%). Intensive and forest cover also explained a significant part of the variance (13% and 8.7%, respectively). As for species richness, the role played by the autocovariate suggested that community stability was spatially dependent (14.5%). The final GLS mixed model ($R^2 = 0.11$) revealed that lower temporal variation in species richness (i.e. higher stability) was detected in landscapes with higher adjacent habitat diversity ($t_{368} = -3.44$, $P < 0.001$). In contrast, temporal variation in species richness was positively related to intensive and artificial cover ($t_{368} = 2.65$, $P = 0.008$; $t_{368} = 4.05$, $P < 0.001$, respectively). No significant effect of forest cover was detected ($t_{368} = -0.73$, $P = 0.46$).

4. Discussion

Heterogeneity within agricultural landscapes was associated with higher species richness. Moreover, the diversity of surrounding habitats was also positively linked with species richness. Such a relationship has already been shown through work focusing on a specific habitat type. In particular, many studies have highlighted that hedges and natural cover around farmland could have a positive effect on species richness (see Hinsley and Bellamy, 2000 for a review). Our results generalize such findings by considering many habitat types and complex lanscapes.

Concerning habitat composition, richer communities were found in landscapes with lower intensive farmland cover. This result is an additional negative relationship previously detected between effects of farmland intensification and birds (Krebs et al., 1999; Donald et al., 2001) and for particular species or specific types of farmland (Verhulst et al., 2004).

The more diverse the surrounding habitat, the more stable was the bird community: i.e. the adjacent habitats had a stabilizing effect on bird communities in agriculturally
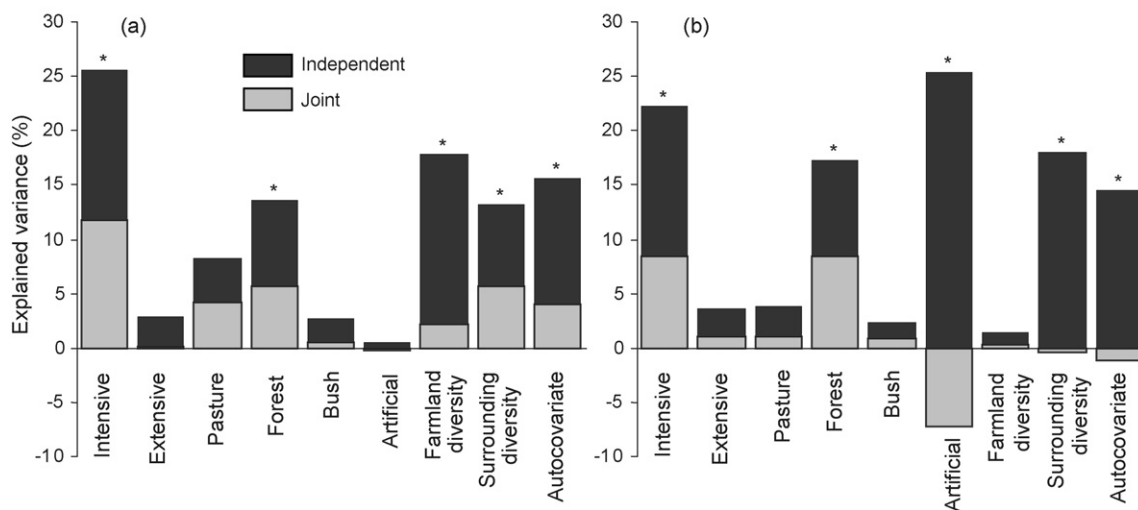

Fig. 2. The independent and joint contributions (given as the percentage of the total explained variance) of each predictor variable estimated from hierarchical partitioning for (a) the species richness and (b) the community stability. Variables marked with an asterisk independently explained a greater proportion of variance than would be expected by chance (with $P < 0.05$ level).

dominated landscapes, in terms of temporal variation in species richness. This further suggests that in open farmland, dynamic processes are strongly linked to diversity in adjacent patches even if species richness is still principally influenced by the main habitat. Indeed, in agricultural landscapes, habitat quality often determines the presence of a species at a given site, and as a consequence, the species richness of a community (Dauber et al., 2003). However, birds are not usually restricted to one habitat patch and often use several patches. In this paper, such a neighbourhood effect is shown to likely affect the farmland community dynamic.

In fact, temporal variation of species richness resulted from both local extinctions and colonisations in the landscape. In some cases, if the number of species remained constant despite a high turnover among the set of species from one year to the next, community stability was underestimated. However, temporal variation of species richness was positively related to both local extinction and turnover rate, and using these two parameters would have led to the same qualitative results: a mosaic of different non-farmland habitats providing for a diversity of ressources, such as refuges and feeding areas, is likely to slow colonisation and extinction rates, and hence stabilize community richness through time. Such neigbourhood effects are likely due to a variety of processes including source–sink dynamics, and lend support to our prediction that agricultural patches do not operate in isolation from their surroundings. Besides, the fact that models were improved when considering spatial autocorrelation, also suggests that, in that context, communities function as metacommunities and that dispersal between sites might be crucial for population persistence at metacommunity level.

The population's persistence for many species in agriculturally dominated landscapes depends on the existence of favourable habitats within the adjacent matrix. In particular, the availability of nesting sites may be a crucial factor that determines the structure of the bird community in agricultural landscapes (Söderström et al., 2003). In this respect, the importance of diversity of vegetation types on marginal farmland for a number of species has been recently highlighted (Woodhouse et al., 2005). No single agricultural factors can be held responsible for all negative impacts on biodiversity but spatial configuration of a species' habitat affects population dynamics, and intra- and inter-specific interactions among individuals. This study suggests that the temporal instability of bird communities due to the homogeneity of intensive farmland could be counter-balanced by the diversity of adjacent habitats and that ignoring composition and diversity of these adjacent patches may hide important features.

Acknowledgements

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