Biological Conservation 176 (2014) 243–251

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Contrasting distributions of grassland and arable birds in heterogenous farmlands: Implications for conservation

Félix Teillard [a,b,*], Delphine Antoniucci [a,b], Frédéric Jiguet [c], Muriel Tichit [a,b]

[a] INRA, UMR 1048 SAD APT, 16 rue Claude Bernard, 75231 Paris Cedex 05, France
[b] AgroParisTech, UMR 1048 SAD APT, 16 rue Claude Bernard, 75231 Paris Cedex 05, France
[c] MNHN-CNRS-UPMC, UMR 7204 CRBPO, F-75005 Paris, France

ARTICLE INFO

Article history:
Received 5 December 2013
Received in revised form 19 May 2014
Accepted 2 June 2014

Keywords:
Heterogeneity
Farmland birds
Specialization
Configuration
Land use
Agri-environment schemes

ABSTRACT

Restoring the heterogeneity of agricultural landscapes has been proposed as a key measure to promote farmland biodiversity. Recent studies, however, warn against generalizing this measure because effects can vary across agricultural contexts and species. We explored the hypothesis that heterogeneity has a negative effect on habitat specialists and a positive effect on generalists. We studied 22 species of common farmland birds belonging to three groups: arable specialists, grassland specialists, and mixed habitat (arable, grassland) "generalist" species. Abundances of these three groups were compared on a nationwide gradient of heterogeneity in France (2006 data), including 510 survey sites. We addressed the heterogeneity of the two main farmland habitats: arable land and grassland. We measured habitat extent (arable/(arable + grassland) ratio) and two heterogeneity components: composition (evenness in the land use proportions) and configuration (probability of adjacency). Although maximal configurational heterogeneity was found at maximal compositional heterogeneity, several landscapes had high compositional heterogeneity but low configurational heterogeneity. The abundance of specialists was strongly correlated with habitat extent and negatively correlated with configurational heterogeneity. It suggests that the most important mechanism influencing their population level could be habitat loss, worsened by fragmentation. Generalist species were more abundant in landscapes with higher proportion of arable land and high configurational heterogeneity, which suggests resource supplementation could be the mechanism that improves their population level. Depending on targeted species, opposite effects of heterogeneity can occur. No unique conservation policy solution to maintain all groups of farmland birds exists, promoting landscapes with various heterogeneity levels will be necessary.

1. Introduction

Agricultural intensification has been associated with a loss of heterogeneity at the landscape level (Robinson and Sutherland, 2002; Sutherland, 2004). Enhancing landscape heterogeneity, therefore, may significantly mitigate biodiversity declines caused by intensification (Benton, 2003; Tscharntke et al., 2005). Several findings, however, advise against generalizing the potential biodiversity benefits of measures that promote heterogeneity in agricultural landscapes. In fact, special attention should be paid to heterogeneity effects that differ according to agricultural context and the degree of species habitat specialization.

Heterogeneity effects can vary according to landscape context. Tscharntke et al. (2005) proposed that local measures to promote heterogeneity in simple landscapes yield the highest biodiversity gains. Empirical findings also support this hypothesis (Roschewitz et al., 2005; Concepción et al., 2008). Batáry et al. (2011b) argue that heterogeneity can be detrimental to specialist species in homogeneous, grassland-dominated landscapes and found that bird species, specialized to extensive Hungarian grasslands, decline with heterogeneity (Batáry et al., 2007). Evidence of heterogeneity effects on large gradients, from grassland-dominated to arable land-dominated landscapes is lacking.

Two components of landscape heterogeneity are explicitly recognized: composition and configuration (Duelli, 1997; Fahrig et al., 2011). A landscape will have high compositional heterogeneity if it has a large variety of land uses in approximate equal proportion. Furthermore, spatial arrangement of land uses in a complex pattern leads to high configurational heterogeneity. A wide range of

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* Corresponding author at: INRA, UMR 1048 SAD APT, 16 rue Claude Bernard, 75231 Paris Cedex 05, France. Tel.: +33 144081775.
E-mail address: teillard@agroparistech.fr (F. Teillard).

http://dx.doi.org/10.1016/j.biocon.2014.06.001
0006-3207/

heterogeneity descriptors has been used in the literature, with no consensual measure. Many authors use the percentage of semi-natural habitat as an indicator of compositional heterogeneity (Billeter et al., 2008; Batáry et al., 2010a). This emphasis on semi-natural habitat assumes that species mainly find resources (e.g., food, nesting habitat) in either natural or semi-natural patches of habitat. The underlying mechanism of the impact of heterogeneity is the loss of those habitats, with fragmentation potentially worsening its effect (Steffan-Dewenter, 2002; Fahrig, 2003). It also assumes that the matrix does not offer any resources (Debinski and Holt, 2000). These assumptions are not accurate for several farmland species, for which agricultural landscape is a mosaic of habitats that offer different resources with different qualities (Duelli, 1997; Law and Dickman, 1998). In these cases, the mechanisms of the heterogeneity impact on species distribution are habitat compensation, complementation, and supplementation (Dunning et al., 1992; Brotons et al., 2005). Compensatory land use provides resources in lower quality than those in ideal land use, while two complementary land uses each contain essential resources. The last mechanism allows species to supplement their resources from nearby patches of alternative land use that has equal quality.

Because species do not have the same resource requirements, the effects of heterogeneity can vary among them. Accounting for species traits is necessary, to understand the mechanisms underlying the landscape heterogeneity effect (Steffan-Dewenter, 2000; McGill et al., 2006). The degree of habitat specialization for a species is particularly important (Andrén et al., 1997). Filippi-Codaccioni et al. (2010) showed that the most specialized bird species were negatively affected by landscape heterogeneity. This result is similar to most findings that show specialist species to be more severely impacted by habitat disturbance, which conversely has a positive effect on generalist species (Marvier and Kareiva, 2004; Schweiger et al., 2007; Devictor et al., 2008). The literature, therefore, suggests the following hypothesis: heterogeneity is beneficial to generalist species and detrimental to specialist species. The mechanisms of these effects remain unclear. Negative effects on specialists could correspond to habitat loss, potentially worsened by fragmentation, and/or detrimental resource compensation (i.e., resource quality is lower in alternative habitat than in ideal habitat). Positive effects on generalists could correspond to resource complementation, supplementation, and/or pure compensation (i.e., similar resource quality is in both alternative and ideal habitats).

Most studies addressing the effects of heterogeneity on specialists vs. generalists have been limited to compositional heterogeneity indicators, such as studies revealing the importance of the proportion of arable lands (Ekroos et al., 2010; Filippi-Codaccioni et al., 2010). Chiron et al. (2010) combined several land uses into a Shannon index of landscape diversity and showed that it decreased colonization rate for specialist species in particular. Brotons et al. (2005) used a steppe/improved pasture ratio to determine whether land uses provided either compensatory or complementary resources to several bird species. These studies did not account for configurational heterogeneity (i.e., for the spatial arrangement of the land uses). Configuration influences the species distribution because it conditions the level of fragmentation and it determines if the land uses and their resources are available within species habitat ranges. Addressing the effects of both composition and configuration is, therefore, necessary to understand the mechanisms of the heterogeneity effects on generalist and specialist species (Dunning et al., 1992).

Here we explored the hypothesis that state opposite effects of heterogeneity on habitat specialists vs. generalists by disentangling the effects of compositional and configurational heterogeneity, in order to unravel the underlying mechanisms. We did this on a nationwide gradient of heterogeneity between grassland and arable land habitats, unlike most previous studies that described landscape composition more precisely but on smaller scales. Specialization was defined within farmland as the frequency of association with sub habitats (Julliard et al., 2006), grassland and arable land. We studied species of a farmland bird community that we discriminated into three groups: two groups of habitat specialists (grassland specialists and arable specialists) and one group of generalists (mixed arable/grassland habitat species).

2. Methods

2.1. The French Breeding Bird Survey

We used data from the French Breeding Bird Survey (FBBS). The FBBS is a nationwide, standardized, monitoring program for which skilled volunteer ornithologists count breeding birds at randomly selected sites each spring (Jiguet et al., 2011b). Surveyed sites are 2 * 2 km squares, where observers carry out 10 evenly-distributed point counts. Point counts are unbounded, observers record every individual bird either heard or seen, along with the distance of contact (<25 m, 25–100 m, >100 m), during a 5-min survey. The ten point counts are surveyed twice in the spring.

We calculated the relative abundance of each bird species at each sample point as follows. Since we focused our study on farmland birds, we only used farmland-dominated sites, i.e. sites with at least five points located within farmland. As each point is surveyed twice a year during the spring, we retained the maximum of both counts. This value corresponded to the yearly local relative abundance per point.

Heterogeneity values were available for 2006. We retained bird relative abundances, surveyed from 2006 to 2008 to account for potential delayed effects. Considering more years also enables to smooth for sampling errors, and for short-term fluctuations in numbers (Jiguet et al., 2011a). The number of surveyed years varied between sites. To avoid pseudoreplication and certain sites contributing more than others towards the effect of habitat extent and heterogeneity, we averaged the local relative abundance per point in sites surveyed more than one year. It resulted in a total of 3787 points located in 510 sites (Fig. 1a, average number of sites per small agricultural region ± standard deviation = 2.15 ± 2.01).

2.2. Trait-based species groups

We focused on a community of 22 common bird species (Table 1), classified as farmland birds by the European Bird Census Council (Vorisek et al., 2010). Within this community, we formed three species groups according to their habitat specialization: grassland specialists, arable specialists, and generalists (mixed arable/grassland habitat species). The main habitat of farmland bird species can influence their response to landscape heterogeneity (Batáry et al., 2007; Fischer et al., 2011) and more generally, similar species can display analogous long term changes (Fuller et al., 1995; Orlowski and Lawniczak, 2009).

To determine the main habitat of each species within farmland, we first computed a continuous Species Specialization Index for grassland (SSIg) for each species. The SSIg was computed similarly to the Species Specialization Index (SSI), which reflects species specialization in larger habitat classes (e.g., farmland, forest, wetland) (Julliard et al., 2006). FBBS and SSI data have already been used in studies testing for landscape heterogeneity effects on birds (Devictor et al., 2008; Filippi-Codaccioni et al., 2010).

We computed SSIg as a weighted mean of species abundance across four sub-habitats within farmland habitat: unimproved grassland, improved grassland, mixed grassland/arable land, and