Original Research Article

Bird metacommunity processes remain constant after 25 years of landscape changes

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A B S T R A C T

Metacommunity theory provides a framework to understand how ecological communities vary in space and time. However, few studies have investigated metacommunity processes in a context of long term changes. Environmental changes can impact species distribution and therefore the structure of metacommunities. Using two complementary methods, this study evaluated the temporal variability of bird metacommunity processes in an agricultural landscape after 25 years of changes in land-cover. Bird and landscape data were recorded in the same locations using a series of 256 point counts in 1982 and 2007. First, variance partitioning was applied to quantify the roles of environmental filtering (i.e. landscape composition variables) and spatial variables to organize bird metacommunities each year. Second, changes in the structure of the bird metacommunity were examined by quantifying three of its components: coherence, species turnover and species range boundary clumping. Our results demonstrate that landscape variables explained slightly more bird metacommunity patterns than spatial variation of unknown origin each year. The bird metacommunity had a Clementsian structure (i.e. grouped distribution of species along environmental gradients) which was correlated with a landscape gradient ranging from open farmland to wooded sites. This structure was similar each year. To conclude, the study shows that environmental filtering with specializations to different habitats is a major process in determining bird metacommunities in landscapes. Moreover, our results suggest that metacommunity structure can remain constant over time despite demographic and environmental changes.

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1. Introduction

A major challenge in ecology is to understand the factors causing community changes in space and time (Rosenzweig, 1995). Various processes have been identified to explain how species from a regional species pool coexist locally. Regional processes operate on a large scale and regulate the arrival of species in local communities (e.g. dispersal and landscape connectivity). Locally, populations are selected through environmental filtering (e.g. foraging and nesting habitats) and biotic interactions. Finally, stochastic colonization and extinction events can also take place (Stegen et al., 2013), particularly at fine scales (Campbell et al., 2010). Assessing the importance of these processes and their responses to environmental change can provide information on community sustainability and appropriate conservation strategies (Diaz et al., 2013).

The theoretical framework of metacommunity ecology synthesizes and improves the understanding of these processes (Leibold et al., 2004; Logue et al., 2011). Two main approaches can be used (Meynard et al., 2013). The first consists in identifying the portion of variance explained by environmental filtering (also called species sorting or niche differentiation) of the proportion of variance explained by the spatial structure using variance partitioning (Cottenie, 2005; Hájek et al., 2011). Interpreting the effect of spatial structure is often difficult (Peres-Neto and Legendre, 2010) as it may result from spatial ecological processes such as dispersal or species interactions, or spatially structured environmental factors not included in the variance partitioning. The second involves the analysis of the metacommunity structure (Leibold and Mikkelson, 2002; Presley et al., 2010). The latter depends on three structural elements (Fig. 1): (a) coherence, which measures the level of structure of species distribution over an environmental gradient; (b) species turnover, which quantifies the number of species replacements between sites; low turnover rates

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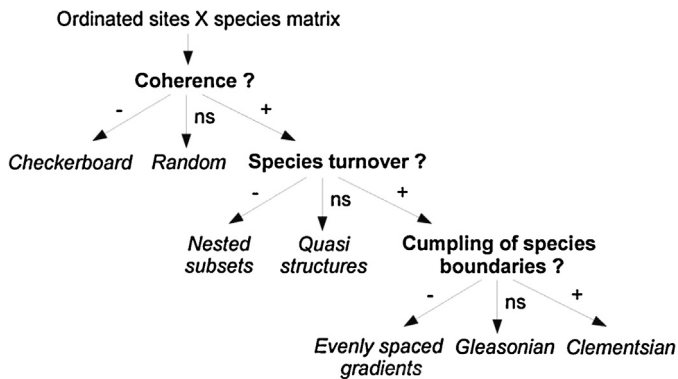E-mail addresses: bonthoux.sebastien@gmail.com (S. Bonthoux), gerard.balent@toulouse.inra.fr (G. Balent).

Fig. 1. Framework for the elements of the metacommunity structure analysis. ns: non significant.

indicate a nestedness pattern; (c) species range boundary clumping, which enables differentiating between Clementsian patterns (i.e. groups of species which show similar responses to the environment) and Gleasonian patterns (i.e. a continuum of gradually changing species composition where species show individualistic responses to the environment). By combining these three structural elements the metacommunity structure can be defined according to several patterns: random, checkerboard, nestedness, evenly spaced, Clementsian, Gleasonian and quasi structures (Fig. 1). It has recently been shown that these two approaches are complementary to understand metacommunity patterns and processes (Meynard et al., 2013; Fernandes et al., 2014).

Given the difficulty to collect temporal data, most studies address metacommunities statically, at a single date. In a dynamic context, environmental changes would be expected to affect the local species distribution and therefore the structure of metacommunities (Fernandes et al., 2014). Understanding these mechanisms at the landscape scale (i.e. a few hectares to a few km^2) is very relevant because it is at this level that territories are managed (Benoît et al., 2012). The few studies that have evaluated changes in metacommunities in the long term have exclusively focused on plants and have provided contrasting results. Keith et al. (2011) found that a Clementsian community structure of woodland plants in England remained constant over a 70-year interval. Similarly, Newton et al. (2012) found no changes in the structure of metacommunities of calcareaous grassland plants. However, Diaz et al. (2013) found a long-term change in a lowland heath metacommunity, suggesting a change in ecological processes. Studies on other taxa are needed to improve the understanding of metacommunity dynamics.

For several decades, many bird populations have been declining in Europe (Gregory et al., 2005; Sanderson, 2006). At a national level, land-use and climate change are known to be major drivers of these demographic changes (Butler et al., 2010; Jiguet et al., 2010). Locally, several studies have highlighted the effects of landscape change on bird communities (Sirami et al., 2007; Wretenberg et al., 2010). Bonthoux et al. (2013) studied bird communities in relation to landscape changes in southwest France between two dates separated by 25 years. They showed that the gamma diversity (i.e. species richness at the study area scale) was maintained but alpha diversity (i.e. species richness at the bird count point scale) decreased. This paper aims to continue this study by assessing the temporal variability of processes structuring bird metacommunities. First, the roles of environmental filtering (i.e. landscape habitat variables) and spatial variables to organize bird metacommunities were quantified through the variance partitioning approach at both dates. Second, the change of the bird metacommunity structure was analyzed in response to environmental changes and in relation to the decrease in

alpha diversity. Specifically, species extinctions can modify metacommunity structure through changes in structural elements (e.g. a decline in coherence).

2. Methods

2.1. Study area, bird and landscape data

The study area is located in the Long Term Ecological Research site of the 'Vallées et Coteaux de Gascogne' (LTER_EU_FR_003, approximately 260–km^2) in southwest France. Landscapes included in this study are heterogeneous and composed of many small wooded areas (a few hectares), crops and grasslands (see Bonthoux et al., 2013 for a more detailed description of the study area and bird and landscape samplings).

A set of 256 point counts was recorded in the same locations in 1982 and 2007. The point counts were at least 250 m apart (mean pairwise distance of 8.4 km). In 1982 and 2007, the presence or absence of bird species was recorded within a 125 m radius (approximately 5 ha) at each point for 20 min. Raptors were excluded from the analyses because of their large home ranges, as well as human-related species because the point counts did not include a human settlement gradient. Species that occurred at only one point count were also excluded from the analysis because they have a strong positive effect on coherence and boundary clumping and can bias results (Presley et al., 2010, see below). In the end, 40 bird species met the outlined criteria in 1982 and 41 species in 2007, of these 38 species were present each year.

Based on aerial photographs and field validation, seven landscape composition variables were calculated for each point count each year: the percentage of crops, semi-natural grassland, wooded fallow, juniper fallow, and woodland, the total length of hedgerow and a Shannon's diversity index based on the percentage of each land use variable. These variables were calculated within a 125 m radius. Pelosi et al. (2014) have shown that bird distributions are mainly influenced by local habitat. As a result of agricultural intensification during the 25-year period, there was a marked increase in crop area (from a mean of 27% in 1982 to 45% in 2007) at the expense of semi-natural grassland (from 33% to 17%). However, the amount of woodland and the length of hedgerow remained stable (from 25 to 27% of woodland between 1982 and 2007, from 169 to 142 m of hedgerow) (Bonthoux et al., 2013).

2.2. Spatial variables

Principal coordinates of neighbor matrices (PCNMs) were used to generate spatial variables. PCNMs are obtained by applying a principal coordinate analysis on a distance matrix between sampling sites. Eigenvectors associated with the positive eigenvalues can then be used as explanatory spatial variables in regression or multivariate analyses (Dray et al., 2006). This method enables spatial patterns to be represented at multiple spatial scales. Eigenvectors associated with high eigenvalues represent broad-scale patterns of relationships among sampling sites, whereas those associated with low eigenvalues represent fine-scale patterns (Griffith and Peres-Neto, 2006). We used the 'PCNM' software package in R (Legendre, 2009) to compute the eigenvectors and the 'packfor' package (Dray et al., 2009) with the forward selection function to select the spatial vectors. Twelve vectors were thus selected as spatial variables.

2.3. Analyses

2.3.1. Variance partitioning

Variance partitioning in 1982 and 2007 was used to disentangle the pure landscape composition effects which were independent of