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Landscape heterogeneity as an ecological filter of species traits

Rémi Duflot [a,b,*,1], Romain Georges [a,1], Aude Ernoult [a], Stéphanie Aviron [b], Françoise Burel [a]

[a] CNRS, UMR 6553 Ecobio, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes Cedex, France
[b] INRA, UR 980, SAD-Paysage, 65 Rue de Saint Brieuc, CS 84215, 35042 Rennes Cedex, France

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ABSTRACT

Landscape heterogeneity is a major driver of biodiversity in agricultural areas and represents an important parameter in conservation strategies. However, most landscape ecology studies measure gamma diversity of a single habitat type, despite the assessment of multiple habitats at a landscape scale being more appropriate. This study aimed to determine the effects of landscape composition and spatial configuration on life-history trait distribution in carabid beetle and herbaceous plant communities. Here, we assessed the gamma diversity of carabid beetles and plants by sampling three dominant habitats (woody habitats, grasslands and crops) across 20 landscapes in western France. RLQ and Fourth Corner three-table analyses were used to assess the association of dispersal, phenology, reproduction and trophic level traits with landscape characteristics. Landscape composition and configuration were both significant in explaining functional composition. Carabid beetles and plants showed similar response regarding phenology, i.e. open landscapes were associated with earlier breeding species. Carabid beetle dispersal traits exhibited the strongest relationship with landscape structure; for instance, large and apterous species preferentially inhabited woody landscapes, whereas small and macropterous species preferentially inhabited open landscapes. Heavy seeded plant species dominated in intensified agricultural landscapes (high % crops), possibly due to the removal of weeds (which are usually lightweight seeded species). The results of this study emphasise the roles of landscape composition and configuration as ecological filters and the importance of preserving a range of landscape types to maintain functional biodiversity at regional scales.

1. Introduction

Agricultural landscapes occupy approximately 75% of Europe (Robinson and Sutherland, 2002), and support a high amount of plant and animal total biodiversity (Benton et al., 2003). Agricultural intensification and land-use changes represent major causes of biodiversity decline in agricultural landscapes (Strijker, 2005). Since the 2000s, maintaining biodiversity in agricultural landscapes has become an important social and economic issue, with a focus on preserving ecosystem functioning and ecosystem services provision (Kleijn and Sutherland, 2003; Le Roux et al., 2008; Millennium Ecosystem Assessment, 2005).

Spatio-temporal landscape heterogeneity strongly influences the species richness and composition of communities, and is consequently an important parameter that should be considered in biodiversity conservation (Fahrig et al., 2011; Huston, 1995; Turner, 1987). In agricultural landscapes, short-term (crop rotation) and long-term (agricultural intensification) temporal changes represent important drivers of biodiversity (Ernoult et al., 2006; Le Feon et al., 2013). Diversity is also influenced by spatial heterogeneity, which is defined as a combination of two components, compositional and configurational heterogeneity (Duelli, 1992; Fahrig et al., 2011). Landscape composition affects diversity as habitat diversity influences plant, vertebrate and invertebrate diversity (Benton et al., 2003; Poggio et al., 2010; Robinson et al., 2001; Woodcock et al., 2010). Landscape configuration which can be measured from the length of edges (or boundaries), influences species movements and spillovers (Blitzer et al., 2012; Brudvig et al., 2009; Concepcion et al., 2012; Tscharntke et al., 2005). However, high landscape heterogeneity may also increase fragmentation *per se* and have negative effects on biodiversity. Hence, biodiversity is expected to

* Corresponding author. CNRS, UMR 6553 Ecobio, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes Cedex, France. Tel.: +33 223 236 663; fax: +33 223 235 026.

E-mail addresses: duflot.remi@gmail.com (R. Duflot), romaingeorges@live.fr (R. Georges), aude.ernoult@univ-rennes1.fr (A. Ernoult), stephanie.aviron@rennes.inra.fr (S. Aviron), francoise.burel@univ-rennes1.fr (F. Burel).

[1] These authors contributed equally to this work. RD and RG designed the experiment, collected data, performed statistical analyses, and wrote the manuscript. Other authors participated in designing the experiment, data collection and writing the manuscript.

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peak at intermediate levels of heterogeneity. Yet, it remains unclear which ecological processes drive species response to landscape heterogeneity components in agricultural areas (Fahrig et al., 2011).

It is generally accepted that functional traits control species responses to landscape heterogeneity gradients (Barbaro and van Halder, 2009; Vallet et al., 2010), and are readily linked with ecological processes (Diaz and Cabido, 2001). Dispersal traits are considered to be the main traits affected by landscape heterogeneity (Hendrickx et al., 2009; Piessens et al., 2004). The phenology (Silvertown and Charlesworth, 2001; Tremlova and Munzbergova, 2007) and longevity (Lindborg, 2007) of plants are also highly sensitive to landscape fragmentation. Therefore, in addition to local abiotic and biotic factors, landscape heterogeneity may be considered as an ecological filter (Tonn et al., 1990), which selects or excludes species from the regional pool according to particular functional traits (Keddy, 1992; Lomba et al., 2011). The species filtered by landscape composition and configuration represent the landscape species pool, with species being further selected by habitat type and local factors to form local species composition and diversity. Hence, it is essential to obtain knowledge about the landscape scale to describe the processes that govern ecological communities from the regional to the local scales.

In recent literature, some studies investigated the effect of landscape heterogeneity on gamma diversity, i.e. the “whole” diversity measured at a landscape scale (Bennett et al., 2006). Traditionally, the dominant “focal patch” approach has been used, which only tests the influence of landscape heterogeneity on a single site/patch (for a review see Thornton et al., 2011). In contrast, the assessment of gamma diversity allows the resulting overall diversity to be viewed, rather than the response of only one patch (Bennett et al., 2006). However, most existing studies that have used this approach, are focussing on a single habitat (Grasslands: Dauber et al., 2003; woodlands: Radford et al., 2005; hedgerows: Ernoult and Alard, 2011; Millan-Pena et al., 2003; crops: Concepcion et al., 2012). Such gamma diversity measures may be referred as “single-habitat gamma diversity”. However, landscapes are mosaics of different habitats, supporting communities of varying species composition. Therefore, single-habitat gamma diversity only partially reflects overall landscape diversity, with the study of total landscape scale diversity being required to consider the diversity of multiple habitats, which we termed “multi-habitat gamma diversity”. Such measure of landscape-level gamma diversity hierarchically depends on local diversity (alpha) and beta diversity among patches of the same habitat types (beta patch) and among habitat types (beta habitat (Crist et al., 2003; Diekotter et al., 2008). Although mosaic-level diversity monitoring is important from a conservation and landscape planning perspective, there are limited studies using this approach (but see Liira et al., 2008).

Here, we investigated the distribution of dispersal, phenology, reproduction and trophic traits for carabid beetles and herbaceous plants along a gradient of spatial heterogeneity in typical western European agricultural landscapes. We evaluated multi-habitat gamma diversity, including crop habitats, to determine i) whether landscape heterogeneity (composition and configuration) serves as an environmental filter for species, ii) which functional traits are affected by the landscape heterogeneity, and iii) whether the observed response patterns could be extended to different species groups (i.e. across taxa).

2. Materials and methods

2.1. Study area

The study was conducted in hedgerow network agricultural landscapes located in the west of France (Fig. 1). These landscapes are typical of western Europe (Baudry et al., 2000) and have been subject to major modifications since the middle of the twentieth century because of agriculture intensification (Baudry and Papy, 2001; Meeus, 1993). The study area is located in a region where dominant agriculture is mixed dairy farming. The farmlands contain annual crops (mostly winter cereals, but also corn), along with temporary and permanent grasslands, and are separated by woodlands and hedgerows (termed woody elements here). These two types of grasslands are comparable in this area, as they are often similarly managed (Roche et al., 2010).

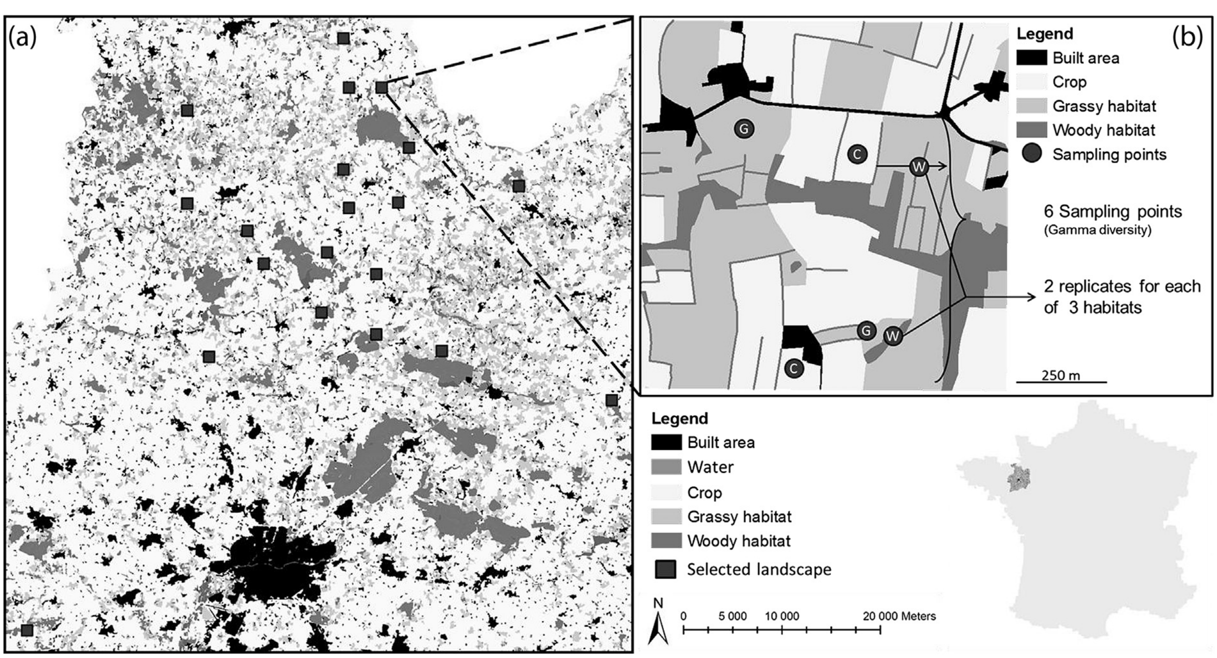

Fig. 1. Map of the study area showing the 20 × 1 km^2 selected landscapes (a) and the hierarchical sampling design of one of these landscapes (b). The sampled cover types are W: woody habitat, G: grassland and C: winter cereal crop.