



Research Paper

Two decades of change in a field margin vegetation metacommunity as a result of field margin structure and management practice changes

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ABSTRACT

Field margins have considerable ecological significance in agricultural landscapes by providing habitat and resources for farmland biodiversity. Few attempts have been made to examine the long term dynamics of multiple vegetation communities in field margins, at the landscape scale. In addition, drivers and processes governing such long term vegetation dynamics are poorly investigated. The aim of the study was to assess whether the diversity and composition of a field margin metacommunity have changed over the last two decades as a result of changes in both structural condition and management of field margins. In total, 309 field margins in north-western France, first surveyed in 1994, were resurveyed in 2015 by using the same protocol. Total species richness (gamma diversity) was stable over time while mean species richness per field margin (alpha diversity) increased. No difference in species composition dissimilarity (beta diversity) was recorded indicating that no biotic homogenization had occurred between 1994 and 2015. Species composition has shifted over time, with a decline of hemicryptophytes and an increase of shade-tolerant species. No change in Ellenberg nitrogen value was observed. Analysis of drivers revealed a significant influence of changes in the structural condition of field margins, i.e. the development of the tree layer, on vegetation diversity. Dominant height of vegetation and tree cover were highest in 2015 compared with 1994. This has likely been driven by a decline in intensity of field margin management. Despite changes in alpha diversity, the field margin metacommunity had a stable Clementsian structure over time, suggesting grouped distribution of species along environmental gradients. This study provides a rare example of the long term vegetation change in field margins in relation with margin structure and management changes, using permanent plots and diachronic data. Results highlight the need to maintain a variety of differently structured and managed field margins to preserve high plant diversity. They underline the need to place conservation strategies in the context of regional-scale processes to ensure the long-term conservation of field margin metacommunities.

1. Introduction

In the second half of the 20th century, agricultural intensification has severely modified agricultural landscapes with deep consequences on the structure and functioning of semi-natural habitats (Tschamtker et al., 2005). In the agricultural landscapes of western Europe, field margins count among semi-natural habitats that have experienced severe loss either by individual farmer initiatives or within organized land consolidation programs (Barr and Gillespie, 2000; Baudry et al., 2000; Deckers et al., 2005). By contrast, there is now a growing recognition that field margins have the potential to play a significant role in environmental protection and biodiversity conservation within intensively managed landscapes through the provision of habitat, shelter and resources for farmland wildlife (Marshall and Moonen, 2002;

Hannon and Sisk, 2009; Vickery et al., 2009). They are recognized to support a wide range of ecological services such as conservation of native flora (Le Coeur et al., 2002), pollination (Morandin and Kremen, 2013) and pest regulation (Bianchi and Wäckers, 2008). Field margins also contribute to species movements by ensuring connectivity through the landscape and may act as a dispersal network (Marshall and Moonen, 2002). Thus, field margins are not only important for the persistence of local communities but also for metacommunity, i.e. a set of interacting local communities that are linked by dispersal, in agricultural landscapes (Ma et al., 2013).

Due to their high conservation potential, a large body of research focused on factors driving biodiversity of field margins. The structural condition, i.e. the physiognomy, of field margins has a strong effect on its value as habitat for plant species. It has been shown that field

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margins with dense shrub and tree layers such as hedgerows are more likely to support shade-tolerant perennial plant species (Hannon and Sisk, 2009). The width and age of field margins have also been recognized as determinants of the diversity of understory plant communities (Roy and de Blois, 2008). At larger spatial scale, landscape heterogeneity and connectivity of the hedgerow network have been shown to influence vegetation diversity within field margins (Davies and Pullin, 2007; Ernoult and Alard, 2011).

Field margins require management to prevent encroachment on adjacent agricultural land (Baudry et al., 2000). Traditionally, tree layer management techniques included hedge-laying or coppicing, applied every 20–40 years (Deckers et al., 2004; Staley et al., 2015). Herbicide use by farmers at the base of the hedge or on a ditch bank is also common to prevent plant species invasion towards their fields. Adjacent agricultural activities (especially tillage, grazing and herbicide drift), together with treatments directly applied to the field margin result in a high level of disturbances, soil nutrient enrichment, with serious consequences for the floristic diversity of these semi-natural elements (de Snoo and van der Poll, 1999; Marshall and Moonen, 2002). While previous work evidenced management practices as a driver of biodiversity loss, the impact of management change on field margin vegetation is poorly investigated, especially in the context of biodiversity conservation.

It is noteworthy that field margin studies have addressed current diversity patterns rather than changes in diversity over time. Changes in diversity and analyses of their drivers are best examined using long term data on community change at multiples site in a landscape (Hédil et al., 2017). But, comparatively with other semi-natural elements such as grasslands and forests, little research has been undertaken on the long-term dynamics of vegetation communities within field margins, perhaps because suitable historic data are rare. One notable exception is the work of Staley et al. (2013) who examined long term vegetation changes, in southern England, by resurveying 357 hedgerows after about 70 years. Results showed an increase in mean species richness (alpha diversity) but a decrease in species composition dissimilarity (beta diversity) with vegetation communities becoming more similar to one another over time, i.e. biotic homogenization. These trends were indirectly associated with both historical and recent hedgerow management as well as eutrophication due to both atmospheric deposition of nitrogen and intensive use of agricultural fertilizers. However, no study directly tested for the effect of changes from i) the structural condition of field margins and ii) management of both the tree, shrub and herb layers of field margins on the dynamic of vegetation communities, using diachronic data.

Analysis of metacommunity dynamic may provide insight into the patterns and processes of several communities and their response to environmental changes, which can in turn inform appropriate conservation strategies over broad spatial scales (Siqueira et al., 2012; Diaz et al., 2013). Leibold et al. (2004) define a metacommunity as a set of local communities of multiple potentially interacting species that are linked by dispersal. They identify four distinct paradigm under which theoretical and empirical work on metacommunity has developed. The ‘patch dynamic’ paradigm suggests that spatial dynamics are dominated by species extinction/colonization events while the ‘species sorting’ paradigm emphasizes grouped distribution of species along environmental gradients. The ‘mass effect’ paradigm focuses on the role of emigration and immigration in the spatial dynamics of communities. The ‘neutral’ paradigm considers all species identical in their ability to move and compete (Leibold et al., 2004). With respect to plants, the sole analyses of long term metacommunity dynamic were undertaken by Keith et al. (2009) and Newton et al. (2012). Results demonstrated that metacommunity structure was maintained over time despite biotic homogenization. The phenomenon of biotic homogenization refers to an increase in similarity in species composition, i.e. a decrease in beta diversity, across a set of communities (Olden and Rooney, 2006). This issue has attracted increasing research interest, as it provides an

indication of biotic impoverishment resulting from environmental changes. However, evidence of biotic homogenization is still conflicting (Newton et al., 2012).

The aim of this study was to evaluate long term changes in meta-community structure and composition of field margins in agricultural landscapes of Brittany, France. The study was based on resurveys of 309 field margins. Specifically, the objectives were to test whether (1) any changes in mean and total species richness, i.e. alpha and gamma diversity, occurred over a period of two decades, (2) community composition has shifted and has led to biotic homogenization, i.e. a decline in beta diversity between 1994 and 2015, (3) metacommunity structure differed between the two sampling periods, and identify (4) which drivers (changes in structural condition and/or management of field margins) were responsible for observed differences. Based upon the results of Staley et al. (2013), I expected that alpha and gamma diversity would increase while beta diversity would decline, providing evidence of biotic homogenization. Following Diekmann et al. (2014), I also predicted that the main driver of shift in species composition and of diversity loss would be soil eutrophication, i.e. management-related factors.

2. Material and methods

2.1. Study area

The study was conducted in the Zone Atelier Armorique (Long Term Ecological Research site, 48° 36′ N, 1° 32′ W), which is located in the northern part of Ille-et-Vilaine in Brittany, north-western France. The climate is temperate oceanic with close to 700 mm of annual precipitation. Average annual temperature is about 12 °C; mean temperature is about 18 °C in summer and about 5 °C in winter. Agriculture is oriented towards mixed dairy farming. The farmlands contains temporary and permanent grasslands (not ploughed for at least 5 years), in addition to winter cereals (wheat and barley) and maize. An extensive hedgerow network (‘bocage’) characterizes the landscape, with relatively small fields (on average 1.3 ha) being separated by woody habitats (hedgerows and woodlands). The hedgerows are rows of oak (*Quercus robur*) or chestnut (*Castanea sativa*) generally planted on an earthen bank 0.5–0.8 m high (Burel et al., 1998)(Fig. A.1).

2.2. Resurvey of field margins

A set of 309 field margins across three contrasted landscapes (107 in landscape A, 106 in landscape B and 96 in landscape C), firstly sampled in 1994, was resurveyed in 2015 using precisely the same protocol. The three landscapes (around 650 ha each) were defined from mapping surveys using a combination of the grain size of the field mosaic, the density of hedgerow network and the relative abundance of grassland versus crop. As the three sites are within 5–10 km from one another, they have a common plant species pool (Le Coeur et al., 1997). In landscape A, the hedgerow network was the densest (115 m/ha). In landscape B, it was intermediate (74 m/ha). Landscape C was a more open landscape with the lowest density of hedgerows (44 m/ha) (Vannier and Hubert-Moy, 2014). Landscapes A, B and C constituted contrasting landscape contexts and were assumed as having different trajectories through time (landscape A more stable than B and C) (Table 1).

2.3. Vegetation sampling

A field margin was defined as one side of the field boundary. So, within a boundary, two field margins were distinguished for vegetation sampling (Fig. A.1). Field margins may differ in their structural condition (presence or not of a ditch, a tree layer, a shrub layer, see Fig. A.2). All vascular understory plants were sampled in 25 m long plot (one plot per field margin) placed in the middle of the field margin to

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