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Connectivity and propagule sources composition drive ditch plant metacommunity structure

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ABSTRACT

The fragmentation of agricultural landscapes has a major impact on biodiversity. In addition to habitat loss, dispersal limitation increasingly appears as a significant driver of biodiversity decline. Landscape linear elements, like ditches, may reduce the negative impacts of fragmentation by enhancing connectivity for many organisms, in addition to providing refuge habitats. To characterize these effects, we investigated the respective roles of propagule source composition and connectivity at the landscape scale on hydrochorous and non-hydrochorous ditch bank plant metacommunities. Twenty-seven square sites (0.5 km^2 each) were selected in an agricultural lowland of northern France. At each site, plant communities were sampled on nine ditch banks (totaling 243 ditches). Variables characterizing propagule sources composition and connectivity were calculated for landscape mosaic and ditch network models. The landscape mosaic influenced only non-hydrochorous species, while the ditch network impacted both hydrochorous and non-hydrochorous species. Non-hydrochorous metacommunities were dependent on a large set of land-use elements, either within the landscape mosaic or adjacent to the ditch network, whereas hydrochorous plant metacommunities were only impacted by the presence of ditches adjacent to crops and roads. Ditch network connectivity also influenced both hydrochorous and non-hydrochorous ditch bank plant metacommunity structure, suggesting that beyond favoring hydrochory, ditches may also enhance plant dispersal by acting on other dispersal vectors. Increasing propagule sources heterogeneity and connectivity appeared to decrease within-metacommunity similarity within landscapes. Altogether, our results suggest that the ditch network's composition and configuration impacts plant metacommunity structure by affecting propagule dispersal possibilities, with contrasted consequences depending on species' dispersal vectors.

1. Introduction

The intensification of farming practices over the second half of the 20th century has caused a major fragmentation of agricultural habitats (Stoate et al., 2001). Fragmentation impacts plant populations through two distinct effects: habitat loss and the increased isolation of remnant habitats (Fahrig, 2003; Fischer and Lindenmayer, 2007). This fragmentation process has caused a major decline in farmland plant species diversity (Andreasen et al., 1996; Luoto et al., 2003; Baessler and Klotz, 2006; Kleijn et al., 2009). In intensive agricultural landscapes, linear landscape elements, such as hedgerows, road verges, grassy strips, and ditches, may represent refuge habitats for various plant communities (Le Coeur et al., 2002; Marshall and Moonen, 2002; Smart et al., 2002, 2006). Ditches, in particular, tend to be the last remaining wet habitats, and may host a variety of plant species, including declining or protected species typical of former wetlands and moist grasslands (Twisk et al., 2003; Biggs et al., 2007; Liira et al., 2008; Herzon and Helenius, 2008).

The availability of good-quality habitats has long been viewed as the limiting factor for the conservation of plant populations in fragmented agricultural landscapes. Habitat degradation, resulting from agricultural and management practices, impedes the settlement, germination, and development of plant species by changing biotic and abiotic micro-site conditions (Bakker and Berendse,

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1999; Henry et al., 2004; Suding et al., 2005). Consequently, scientific studies have mostly focused on the ecological processes determining plant community structure at the alpha scale in order to offer appropriate local management directives. But such directives sometimes proved to be ineffective: agri-environmental measures designed to restore the habitat quality of ditch banks, for example, failed to improve plant species richness in the Netherlands (Kleijn et al., 2001; Blomqvist et al., 2009). These observations suggest that other processes, operating at the landscape scale, could conceal factors acting at the local community scale. Some studies pointed at the need for a higher sampling scale, the metacommunity, in order to study these processes (Leibold et al., 2004; Bennett et al., 2006). Work carried out in various habitat types have highlighted the relevance of this gamma scale (Dauber et al., 2003; Ernoult and Alard, 2011; Concepción et al., 2012).

Metacommunity diversity and structure are shaped by the interaction of habitat heterogeneity and species dispersal (Mouquet et al., 2006). Landscape heterogeneity has especially been shown to enhance biodiversity in agricultural landscapes (Benton et al., 2003). Additionally, in fragmented areas, remnant habitat patches may be highly heterogeneous, causing a strong divergence in the composition of local communities, and thus inducing increased landscape-moderated within-metacommunity dissimilarity (Tscharntke et al., 2012). In addition, the amount of dispersal between remnant patches may strongly impact these dynamics (Mouquet and Loreau 2003; Mouquet et al., 2006). Seed-limitation, in particular, is a well-known process that occurs when populations have fewer individuals than they could potentially host because propagules do not reach saturation densities (Tilman, 1997; Zobel et al., 2000; Clark et al., 2007). At the metacommunity scale, dispersal limitation is especially expected to enhance divergence between local communities, further reducing their similarity and resulting in a more heterogeneous metacommunity (Mouquet and Loreau 2003, Tscharntke et al., 2012).

The distance to nature reserves as species-rich propagule sources has been shown to have a negative influence on the plant species richness of both restored and non-restored ditch banks plant communities at relatively short distances, supporting this dispersal limitation hypothesis (Kohler et al., 2007; Leng et al., 2009, 2010). However, these studies were restricted at the local community scale, and did not dealt with landscape composition and connectivity impact on metacommunity structure. Moreover, the vast majority of ditches found in agricultural areas of Western Europe are located within "ordinary" intensive agricultural landscapes, which are distant from nature reserves. Within these landscapes, propagule sources for ditch plant communities are diverse. Surrounding land-cover elements host specific communities that represent propagule reservoirs for nearby ditches (grassland plants, weeds originating from crop fields…). But they may also impact ditch bank plant communities themselves by influencing ditches' management intensity and regime, and consequently these communities' propagule source potential for nearby ditches (Le Coeur et al., 1997; Kleijn and Verbeek, 2000). Presence of propagule sources is necessary for enabling colonization, but not sufficient in itself; connectivity of these sources with target habitats is also required. Landscape connectivity, defined as the way landscape elements facilitate or impede the dispersal of individuals (Taylor et al., 1993), may determines movement possibilities between sources and target ditches. Disentangling the respective roles of connectivity and propagule sources composition could provide a better understanding of the processes driving ditch bank plant metacommunity structure.

Several studies have stressed the need to incorporate more functional information into the measurement of landscape connectivity, taking into account processes that drive the dispersal of individuals (Tischendorf and Fahrig, 2000). Plants depend on various dispersal vectors that impact species' response to landscape habitat composition and connectivity. In drained lowlands, the presence of water in ditch networks offers important corridor potential for hydrochorous species (Ozinga et al., 2004; Vogt et al., 2004; Soomers et al., 2010, 2013; Van Dijk et al., 2013), especially as they provide an effective and long-distance dispersal of plant propagules (Nilsson et al., 2010). However, propagules may also be dispersed by other vectors, such as wind or animals (Ozinga et al., 2004). Non-hydrochorous species may be less dependent on the ditch network than hydrochorous ones; hence, these vectors might disperse propagules originating from seed sources other than ditch bank plant communities, located within the adjacent landscape mosaic.

In the present paper, we investigated the respective roles of the ditch network and the surrounding landscape mosaic on the structure of ditch bank plant metacommunities at the gamma scale, based on a dataset collected in an agricultural lowland of northern France. We hypothesized that plant metacommunity structure may respond differently to elements belonging to the landscape network or the landscape mosaic, depending on species dispersal vectors.

Our hypotheses were as follows: (*i.*) As we supposed that ditch bank metacommunities are dispersal-limited, dispersal may therefore be an important driver for ditch bank plant metacommunity structure. Metacommunity species richness and composition, along with the similarity between local communities, may be dependent on the presence and connectivity of propagule sources within ditches. (*ii.*) Water-dispersed plant species would be more sensitive to the composition and connectivity of the ditch network, whereas non-hydrochorous species would primarily rely on the composition and configuration of the landscape mosaic.

2. Material & methods

2.1. Study area

The study area is located in an agricultural lowland of northern France (between 50° 38′ 36.72″ N, 2° 46′ 28.23″ E and 50° 32′ 50.09″ N, 2° 35′ 40.70″ E), and encompasses an 83 km^2 area. This area is characterized by flat topography. Large agricultural fields (mostly crop and vegetable cultures) dominate the landscape (62.4%), while remnant semi-natural areas (grasslands, woodlands, fallow lands) are scarce (15.3%) and highly fragmented. Hedgerows are also rare. However, a dense and well-connected drainage ditch network remains, which covers 642 km of the study site (Fig. 1). Three categories of ditches were delineated based on their size and location.

First, running water ditches ("RW") are the largest and the only ditches with a defined current orientation. They exhibit the highest water levels. The second category includes ditches located along road verges ("RO"), which are of intermediate size. The third category encompasses all the remaining ditches, mostly located between agricultural fields ("AF"). These ditches are more variable in size, but most of them are shallow, as they tend to get clogged. "RO" and "AF" ditches exhibit similar mean water levels and mean percentages of emerged bottoms. Mean dimensions and water levels measured for the three ditch categories are presented in Table 1. These three ditch categories are subject to different management actions; "RW" ditch banks are generally mown once a year, "RO" ditch banks are mown two to three times a year, and "AF" ditch bank management varies depending on the landowner. Numerous culverts are located in the network (mean culvert density of ditches: 7.3 culverts/km). Water levels are higher in autumn and